F THE NORTH SASKATCHEWAN

I THE DISPERSION OF AEDES

by

Waldemar Klassen

DEPARTMENT OF ENTOMOLOGY

University of Alberta

April 1959

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THE UNIVERSITY OF ALBERTA

THE INFLUENCE OF THE NORTH SASKATCHEWAN RIVER VALLEY ON THE DISPERSION OF *AEDES*.

A DISSERTATION

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE.

DEPARTMENT OF ENTOMOLOGY

by

WALDEMAR KLASSEN

EDMONTON, ALBERTA

APRIL, 1959.

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES

The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled .....

.....The influence of the North Saskatchewan River Valley.....

.....on the Dispersion of Aedes.....

submitted by .....Waldemar Klassen.....

in partial fulfilment of the requirements for the degree of Master of .....Science.....

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Date.....April, 1959.....

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ABSTRACT

Observations were made on two appearances of adult mosquitoes in the river valley within the city of Edmonton. These appearances are unusual in that they occurred in the center of an area in which larvae were killed.

During the week preceding May 17, 1958 large numbers of mosquitoes, mostly Aedes cataphylla Dyar appeared;and during the week preceding June 3, 1958 large numbers of mosquitoes, mostly of Aedes fitchii F.& Y., Aedes excrucians Wlk. and Aedes stimulans Wlk. appeared in the above mentioned section of the river valley. The route of entry of mosquitoes into the city was determined from a consideration of wind data from those hours when extreme environmental conditions would not suppress spontaneous mosquito activity, from a consideration of optomotor theory, vertical distribution, energy requirements of flight, distribution of adult mosquitoes within the city and from a meteorological study of the study area. The river valley was found to be a favourable and the only possible route of mosquito movement into the city of Edmonton.

Some extensions to optomotor theory were made.

ACKNOWLEDGEMENTS

I wish to indicate my gratitude to Mr. J. A. Shemanchuk for providing indispensible equipment and for his helpful suggestions. Miss J. C. Shore devoted much of her time to typing my correspondence. Professor B. Hocking, Dept. of Entomology, University of Alberta made many helpful suggestions during this study; without his help no results would have been realized. Dr. G. E. Ball and Dr. W. G. Evans of the Dept. of Entomology, University of Alberta often discussed this work and underlying scientific attitudes with me. Dr. Kalmus, Galton Laboratory, London stimulated my interest in insect behavior. Mr. L. B. McHattie of the Meteorological Branch, Dept. of Transport, Ottawa, Ontario offered very helpful advice regarding micro-meteorological problems. Locally Mr. William Stewart, Mr. H. P. Wilson, Mr. J. Kiniski and Mr. R. Stark have given me material aid and also have discussed problems in micrometeorology with me. Iryl Miller, Parks Dept. introduced me to the terrain and helped me set up the meteorological apparatus. Mr. Dave. Harrington, Wetaskiwin showed the terrain to me from the air. I have consulted Miss Z. Hyduk and Mr. James Pounder of the Dept. of Mathematics, University of Alberta, and Dr. A. B. Bhatia, Dr. J. H. Harrold and Dr. G. Garland of the Dept. of Physics, University of Alberta. Mr. A. Laycock of the Dept. of ~~Geology~~ Geography provided some references. Mr. P. H. Bouthillier of the Faculty of Engineering secured some contour maps of the city for me. The Faculty of Engineering loaned a transit to me. Mrs. Ted. Gardiner, 13837 Summit Drive, Edmonton, Alta. donated electrical power for the operation of a mosquito trap. The management of the Mayfair Golf Course allowed me to use their power source and to set up weather instruments on their property. The management of the Highlands Golf Course

allowed me to set up weather instruments on their property. The Dept. of Physiology allowed me to use their workshop. My fellow graduate students have offered much advice, criticism and help. The Parks Dept. of the city of Edmonton provided transportation, equipment and financial assistance.

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1. GENERAL SECTION- REVIEW OF LITERATURE

1.1. DISPERSION: HISTORICAL.

The dispersion of insects has been the subject of much work and speculation. Wolfenbarger (1946) wrote an extensive review of this subject. This author also fitted the data which he reviewed with empirical mathematical relationships relating the density of insects to distance from their source. Kettle (1950) studied the dispersion of the midge Culicoides impunctatus Goetghebuer and also fitted the regression of numbers of midges with distance from source with an empirical mathematical expression. Further Kettle stated that the decrease in density was due to two separate processes: 1) Dilution - the spreading of a population over an area of increasing magnitude.

2) Mortality - the death or going to earth of some adults.

Wadley (1957) discussed in detail the assumptions underlying mathematical equations of dispersion - as Andrewartha and Birch (1954) had done ~ in lesser detail.

Dispersion of leaf hoppers was treated as a random process by Frampton et al. (1942) who also derived an equation based on this assumption. Dobzhansky and Wright (1943) from their study of Drosophila psuedoobscura concluded that dispersion is random with respect to direction and to other members of the population. Davidson and Andrewartha (1948) from their study on Thrips imaginis concluded that "the activity of the thrips in seeking new places to live was independent of the density of the population and by inference equally independent of any external stimuli..."

It has been shown however that movements of at least some insects may not be considered random. Several books have been written on the

orientation and directed movements of animals; most recently Fraenkel and Gunn (1940) and Carthy (1958) have written treatises on this subject.

Kennedy (1939) showed that Aedes aegypti females orient upwind when flying at certain windspeeds and heights above the background, and under a different set of conditions orient and fly downwind. Kennedy also described other flight responses of Aedes aegypti, and in his 1951 paper he extended this optomotor theory of flight regulation to all combinations of heights above the background and windspeeds. The work of Kalmus (1948) lends support to Kennedy's theory. Orientation to wind has been described from field observations by Kennedy (1951) in locusts. The orientation of hovering insects to wind has been described by numerous authors. (Nielsen and Greve, 1950; Downes, 1958)

Much information has been accumulated regarding the passive transport of insects by wind. That insects may be transported long distances by wind, and that meteorological processes cannot be ignored in the study of insect dispersion is established. (Coad, 1931; Elton, 1925; Felt, 1925, 1926, 1928, 1938; Freeman, 1945; Glick, 1939, 1957; Greenbank, 1956; Hardy and Milne, 1937, 1938a, 1938b; Henson, 1951; Smith et al, 1956; Wellington, 1945a, 1945b, 1945c.)

Clearly the movement of insects which orient to a fairly constant stimulus and the movement of insects transported en masse by wind will transgress the theoretical or empirical mathematical relationships described. To understand dispersion in such cases one must know something about intrinsic flight ranges, and orienting mechanisms and meteorological processes.

The flight range of mosquitoes and other insects has been studied

quite extensively. Hocking (1953) reviewed this subject. Moreover this worker has devised and successfully employed an intrinsic method of measuring the distance an insect can fly between feedings. He demonstrated that many Aedes mosquitoes can fly between 30 to 40 air-miles between feedings. It is obvious, however, that the displacement of a flying insect in the field will not only depend on the energy supply, but also on the environmental factors which orient the insect, the insect's behavior in relation to the direction of the wind and the insect's air-speed. Moreover to predict the movement of an insect in the field one must possess a knowledge of the insect's reactions to various environmental variables, and especially to those which influence the displacement of the insect.

Much of the literature before 1944 on dispersion patterns and flight ranges of mosquitoes has been reviewed by Eyles (1944). Table 1 is based on his review. The available literature not included in the review by Eyles and that published after 1944 is summarized in Table 2. Only those papers containing meteorological information are included in these tables.

In order to determine the influence of wind on dispersion, fairly high recoveries are required. Many authors have pointed out that their data were too inadequate to draw binding conclusions. The tables indicate that mosquitoes flew in all directions with respect to the wind as measured at one point. However in most instances the greatest numbers of mosquitoes were recovered downwind. Usually those taken several miles from the source apparently went downwind. In instances where upwind flight was more marked than downwind flight, windspeeds if given were quite low.

Table 1. The dispersion patterns of mosquitoes according to the review by Eyles (1944).

Author	Species	Upwind	Downwind	Remarks
LePrince 1912	Anopheles albimanus Wiedemann	Flew 1 mi.		4 mi.p.h. wind.
DeMeillon 1937	A. funestus		1 mi.-2.8 mi.	3 specimens tagged.
DeMeillon 1937	A. funestus	<0.75 mi.		1 specimen.
Adams 1940	A. funestus and A. gambiae	< 4.5 mi.	3.25 mi.	Other specimens were seen flying with wind.
DeMeillon 1937	A. gambiae		<2 mi.	8 specimens recovered.
Adams 1940	A. funestus and A. gambiae	< 1.5 mi.	4.25 mi.	
Wenyon 1921	A. maculipennis Meigen		1; 2; 3 mi.	
Swellengrebel 1929	A. maculipennis atroparvus Van Thiel		< 8.7 mi.	Many more recovered downwind than upwind.
Russell and Santiago 1934b	A. minimus flavirostris Ludlow	< 0.25 1♀	<1.4 mi. 7♀♀	Strong wind.
Low 1925	A. pharcensis Theobald		5.6 mi.	
Rickard 1928	A. psuedopunctipennis Theobald	<3.7 mi	<3.7 mi.	Mostly upwind.

Table 2. Summary of Published Information on Dispersion of Mosquitoes.

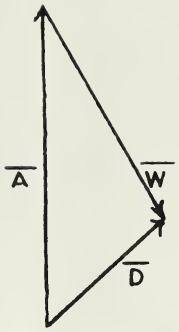
AUTHOR	SPECIES	METHODS	TOPOGRAPHY	METEOROLOGY	PHYSIOLOGICAL STATE-AGE	CONCLUSIONS AND REMARKS
Davis 1901		Field observations; well defined source.	Desert.			Slow, steady breezes brought large numbers of mosquitoes over desert from source 22 miles distant. High winds brought few.
Felt 1904	Aedes sollicitans*, Aedes contator*					"...both of which, as demonstrated by Dr. Smith, are capable of lying or drifting with wind to a distance of 40 miles..."
Hearle 1926	Aedes aldrichi Aedes vexans	Field observations; well defined source.	Fraser valley	Warm moist northerly winds.		Flew north with wind. "...only particularly favourable conditions will entice appreciable numbers into the open any great distance from the protection of woods, raspberry plantations and other cover."
Rees 1935	Aedes dorsalis	Field observations; defined source.	Level plain between mountains.	Slight breeze to east.		Slow movement west against wind from 5-8 mi.
Stage et al. 1937	Aedes vexans Aedes aldrichi	Tagged adults.	Columbia River valley.		Newly emerged.	Upwind and downwind movement. According to the map on flight range, the movement generally took place along the tributaries.
Clarke 1943	Aedes vexans Culex pipiens etc.	Tagged adults.		Wind S-SW variable speed.	Newly emerged.	Flight has strong downwind tendency. One recovery was made 14 mi. downwind from source; windspeed < 34 m.p.h.
Russel et al. 1944	Anopheles culifacies	Tagged adults.	Flat featureless area; two winding streams.		Variable ages.	251 recaptured in downwind quadrant; 69 in upwind quadrant; 77 and 68 in across wind quadrants. < 1.75 mi.
Bonnet and Worcester 1946	Aedes albopictus	Tagged adults.	"Y"-shaped valley; wooded with open areas.		Maintained in cages till needed.	Flew up to 200 yards into the wind.
Causey and Kumm 1948	Haemagogus spegazzinii Aedes leucocelaenus, etc.	Tagged adults.	Patches of forest; small streams.	Wind S-E.	Age unknown.	Flight had downwind bias.
Causey and Kumm 1948	Similar experiment					Flight had upwind bias. Authors suggest that recoveries are too low to permit such interpretation.
Reeves et al. 1948	Culex tarsalis	Tagged adults	Level agricultural district.	NW variable winds.	Variable age.	Upwind flight < 1.4 mi.
Garret-Jones 1950	Anopheles pharcensis Culex sp.	Field observations	Desert.	Strong NE winds		Two separate migrations with wind by moonlight and described as "..coming in a cloud of vapour from the north, which looked like a dust storm by moonlight."

1.2. OPTOMOTOR THEORY AND DISPERSION.

1.2.1. The Optomotor Theory of Insect Behavior in Relation to Windspeed and Height.

The relationship between wind and mosquito behavior is complex. However optomotor theory has been extended to deal with a mosquito's behavior at all heights above the ground and at all wind speeds. Kalmus (1948) suggested that movement across an insect's retinal element is resolved into two vectors: a translational vector parallel to the insect's longitudinal axis, and a rotational vector perpendicular to the insect's longitudinal axis. The insect's brain sums over the whole visual field all the translational vector components from all retinal elements to give the "apparent translation", $\bar{T}$; and the insect's brain sums over the whole visual field the rotational vector components from all retinal elements to give the "apparent rotation," $\bar{R}$. Further the insect usually behaves in such a manner that the sum of the rotational vectors ("apparent rotation") $\bar{R}$ is zero. Explicitly transverse motion is not tolerated (Fig. 1).

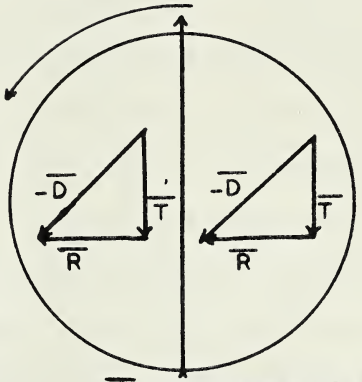
Kennedy (1940, 1951) found that Aedes aegypti females, 10 cm. above a stationary background, orient into the wind when the wind velocity nears 10 cm./sec. We can derive from Kalmus' theory that insects orient into the wind because this response makes the sum of the rotational vector components zero. Kennedy's experiment shows that females of Aedes aegypti require minimal stimulatory rotational retinal angular velocity of less than 1 radian per second. If a mosquito travels at a given ground velocity, the apparent velocity of the images is inversely proportional to the height of the mosquito above the ground. Thus if the mosquito is near the ground, the objects appear to move faster than if the mosquito is at a greater altitude. A mosquito flying under these conditions, but across wind, could climb to a height above which the apparent movement across the ommatidia (rotational vector) would be less than the minimum stimulatory rotational retinal



$\overline{A}$- Insect's velocity

$\overline{W}$- Wind's velocity

$\overline{D}$ - Resultant displacement



$\overline{T}$- Translational vector

$\overline{R}$ -Rotational vector

$-\overline{D}$- Vector of movement

Fig. I. Resolution of the vector of movement by an insect according to the theory of Kalmus. The circle represents a ventral view of an insect's head with a line between the eyes. The vector of movement and its components are shown on each eye. The arrow outside of the circle indicates the direction in which the insect will rotate to make the rotational vectors zero.

velocity (Fig. 2). Kennedy (1951) calls this height the "maximum compensatory height," because above this height the mosquito, regardless of its orientation, will never receive an adequately strong stimulus to make it orient to the wind. i.e. to respond in such a manner that the rotational vector will become zero. This maximum compensatory height, R_R, may be calculated from the expression $V_R = \omega_R R_R$ where V_R is the transverse component of the mosquito's ground velocity ($\leq$ wind velocity) and ω_R is a constant, the minimum stimulatory rotational angular velocity. It must be clearly understood that this expression pertains to the rotational vector of relative motion and not to the translational vector of relative motion.

Kennedy also found that Aedes aegypti females 10 cm. above the stationary background controlled their airspeed so that regardless of the windspeed, the translational ground velocity of the mosquitoes was 17 cm./sec. This experiment suggests that mosquitoes have a preferred translational velocity. Emphasis must be laid on the fact that the rotational and translational velocities are distinct. In still air and over a stationary background, the magnitude of the translational groundspeed, V_{PT}, necessary to produce the preferred translational angular velocity, ω_{PT}, of a mosquito flying at any altitude may be calculated from the expression: $V_{PT} = \omega_{PT} R_{PT}$ where R_{PT} is the preferred height of flight (Fig. 2).

Kennedy performed another experiment. This worker found that Aedes aegypti females at 10 cm. altitude and in still air over a stationary background flew with a groundspeed of 17 cm./sec. If the striped background were then moved in a direction opposite to the mosquitoes' direction of flight, all mosquitoes would turn around and fly with the stripes before the stripe speed reached 13 cm./sec. to 17 cm./sec. In other words Aedes aegypti 10 cm. above a background will not tolerate a translational velocity

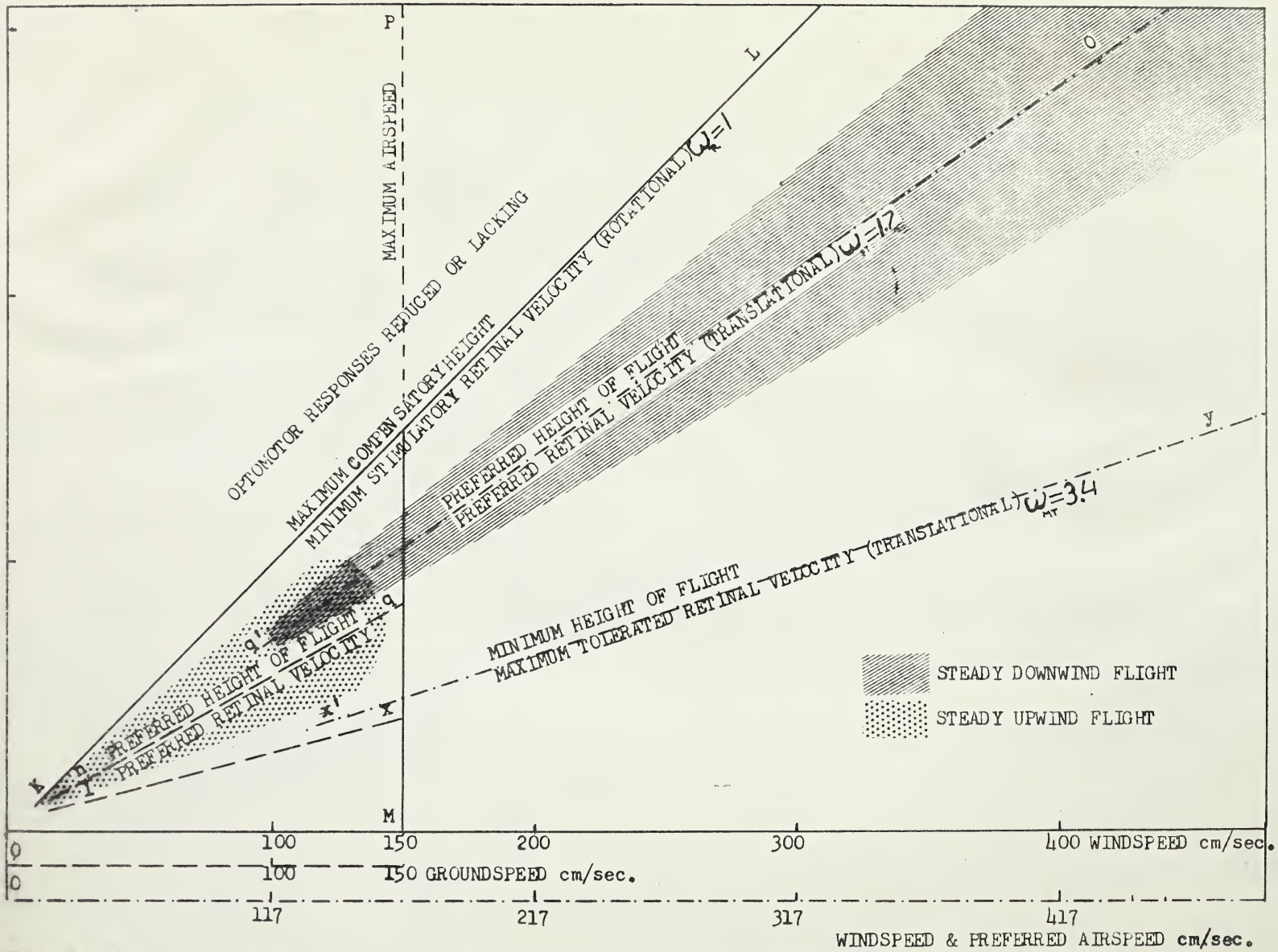


Fig. 2. Flight behaviour diagram of Aedes aegypti based on the data of Kennedy.

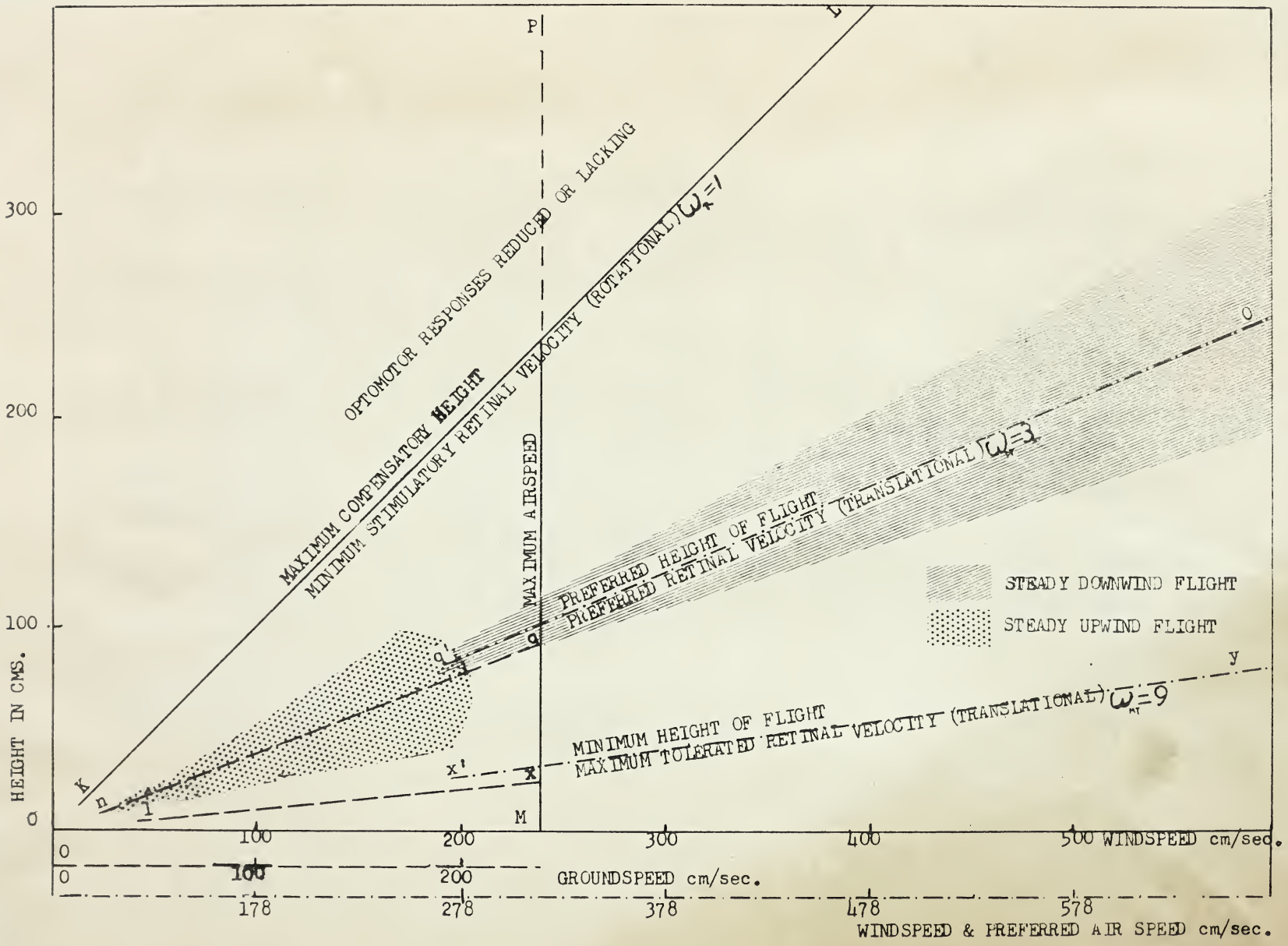


Fig. 3. Flight behavior diagram of Aedes punctor based on the data of Hocking.

greater than 34 cm./sec. (= an angular velocity of 3.4 radians/sec.) This maximum tolerated translational velocity V_{MT} (= ground velocity) may be calculated from the expression $V_{MT} = \omega_{MT} R_{MT}$ where ω_{MT} is a constant, the corresponding maximum tolerated translational angular velocity, and R_{MT} is the minimum height at which female Aedes aegypti will fly.

For Aedes aegypti the values of the constant according to Kennedy's data are: $\omega_R <$ 1 radian/sec.

ω_{PT} = ca. 1.7 radians/sec.

$\omega_{MT} <$ 3.4 radians/sec.

Hocking (1953) worked with northern Aedes species. The following values of the constants have been estimated from his data for Aedes punctor Kirby: ω_{PT} = ca. 3 radians/sec.; ω_{MT} = ca. 9 radians/sec. I am assuming that ω_R is the same as for Aedes aegypti.

Figures 2 and 3 show graphically the relationship between ground velocities and altitudes. Altitude of flight is plotted on the ordinate. On the abcissa windspeed and groundspeed are plotted. Two assumptions have been made: the preferred airspeed of Aedes aegypti is 17 cm./sec., and the preferred airspeed of Aedes punctor is 78 cm./sec.

To the right of the line MP and below the line KL only downwind flight and downwind displacement are possible. Kennedy found that a mosquito in forward flight will not allow herself to be carried backwards; since the mosquito will respond in such a manner that the sum of the rotational vectors will be zero (strictly, $\pm$ reflex threshhold), only downwind flight is possible. For this region, then, the preferred airspeed (cruising speed) plus windspeed equal the groundspeed. This value of the groundspeed may be used to calculate the

preferred height of flight and the minimum height of flight. In the region between the lines KL and lx, and to the left of MP, the mosquito may fly upwind. Upwind flight is possible because in this region of the diagram the airspeed of the mosquito can exceed the windspeed. Upwind orientation would keep the sum of the rotational vectors equal to zero. Clearly the groundspeed of the mosquito is under the control of the mosquito. The mosquito will regulate her groundspeed so that she flies at her preferred retinal velocity. No allowance for windspeed, therefore, need be made to calculate values of R_{PT} and R_{MT} respectively.

Contra Kennedy (1951), the maximum compensatory height is the same for upwind and downwind flight; because the rotational retinal velocity vector is produced entirely by the wind i.e. the movement of a mosquito with constant orientation will in no instance contribute to this rotational vector. Above the line KL the mosquito, according to Kennedy's theory, will be totally unresponsive to transverse movement and its direction of orientation will be random; the mosquito's displacement will have a downwind component equal in magnitude to the windspeed.

Stable downwind flight will occur only near the line q'o. Stable upwind flight will occur only near the line nq. Just to the left of the line MP, the mosquito must fly near her maximum airspeed; and flight will be unstable. Below the lines lx and x'y only exceedingly unstable flight can occur, i.e. either climbing or settling. In summary a mosquito can have stable flight only in the region above KL or along the lines nq and q'o. Mosquitoes in any other region of the behavior diagram will either climb above KL, or fly to nq and q'o or they will settle.

Some parenthetic remarks regarding these behavior diagrams are in order. The values of ω_R and ω_{MT} are maximum observed values. The corresponding altitudes are therefore minimum altitudes; and the corresponding retinal velocities are maximum retinal velocities. Hassenstein (1958b) studied the optokinetic reactions of the weevil Chlorophanus viridis. He found that when every other ommatidium was stimulated the "strength" of the optokinetic response increased with the logarithm of the angular velocity from 2°/sec. to 40°/sec., reached a maximum at 50°/sec., and declined with the logarithm of angular velocity between 100°/sec. and 2000°/sec. However if all ommatidia were stimulated, the "strength" of the optokinetic reaction increased with the logarithm of the angular velocity from 0.04°/sec. and reached a maximum at 100°/sec. The "strength" of the optokinetic reaction can be calculated from Reichardt's formula $f(\omega_R) = k\left(e^{-\frac{\Delta\varphi}{\omega_R \tau_E}} - e^{-\frac{\Delta\varphi}{\omega_R \tau_D}}\right)$ (Hassenstein, 1958b) where $\Delta\varphi$ is the angle between successive stimuli, ω_R is the angular velocity, τ_E and τ_D are time constants. The constant k is calculated from the expression $k = k_\perp \frac{\sigma^2}{\pi \tau_E \tau_D}$ where σ is a constant related to the distribution of strengths of successive stimuli, and $k_\perp$ is the ratio τ_E / τ_D .

The "strength" of the optokinetic response is dependent on the ommatidial angle $\Delta\varphi$. The ommatidial angle of Chlorophanus weevils is 6.8°. Judging from Sato's diagrams (Sato, 1950) the compound eyes of a female Culex pipiens var. pallens occupy about one fourth of the surface area of a sphere. Since there are about five hundred facets per eye, 4000 facets would constitute a sphere. Hence each ommatidium occupies about $\frac{4\pi}{4000}$ = 0.00314 steradians. Hence $\Delta\varphi$ = ca. $\sqrt{0.00314}$ radians = ca. 0.056 radians = ca. 3.2 degrees. A rough estimate of angular velocities

required to produce optokinetic responses of equivalent "strengths" in Chlorophanus and mosquitoes can be made if we assume that the value of is the same for both.

Values of ω_R for Chlorophanus below the value of about 40° may be substituted into the equation $\frac{\Delta\Phi_c}{\omega_{Rc}\tau_E} = \frac{\Delta\Phi_m}{\omega_{Rm}\tau_E}$ where $\Delta\Phi_c$ is the ommatidial angle of Chlorophanus, $\Delta\Phi_m$ is the ommatidial angle of the mosquito, and ω_{Rc} and ω_{Rm} are the corresponding angular velocities. It follows that for an optokinetic reaction of given "strength" at a given angular velocity in Chlorophanus, a reaction of equal strength would be evoked in the mosquito by an angular velocity $\frac{3.2}{6.8}$ times as great as that to which Chlorophanus responded. For example, an angular velocity of 10°/sec. perceived by Chlorophanus would produce an optokinetic reaction in Chlorophanus equal in strength to that produced in the mosquito by an angular velocity of 4.7°/sec. The value of ω_R 1 radian per second (57.3°/sec.) for Aedes aegypti seems therefore to correspond to the angular velocity necessary to produce a maximum optokinetic response. If a behavior diagram for Chlorophanus were made, the maximum stimulatory height might be calculated using $\omega_R = \frac{2}{57.3}$. Hence if the rotational vector had a magnitude of 100 cm./sec., upwind orientation should be possible up to a height of 2870 cm.; the tendency to orient upwind would be greatest at a height of 115 cm. ($\omega_R = \frac{50}{57.3}\frac{\text{radian}}{\text{sec.}}$). To be explicit we might expect some individuals of a population of Chlorophanus to orient up to a height of 2870 cm.; greater deviations from the wind direction would occur with height. Doubtless a population of Aedes aegypti would behave in a similar manner.

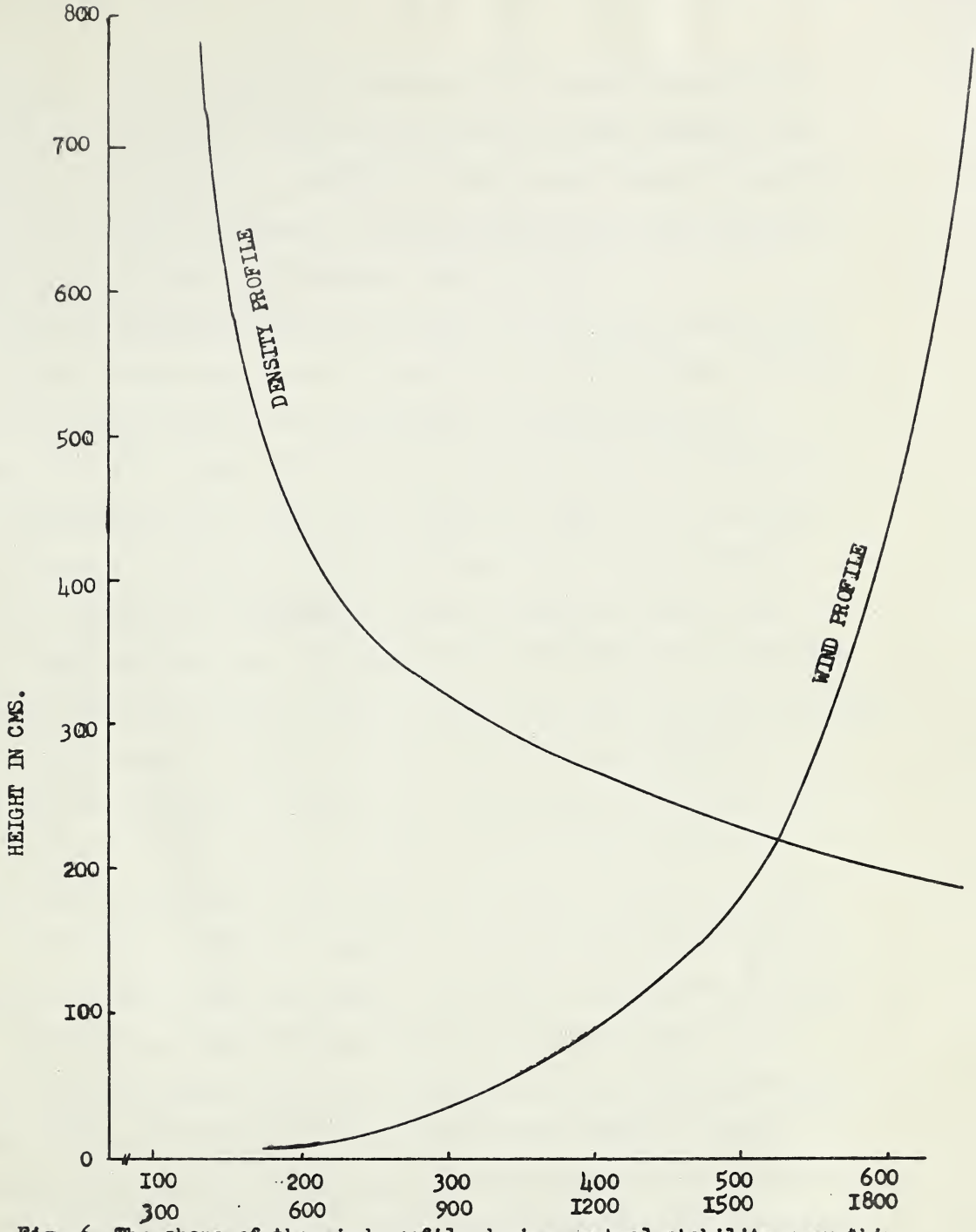


Fig. 6. The shape of the wind profile during neutral stability over thin grass 10 cm. high. (Sutton, 1953) And the shape of the vertical distribution profile of mosquitoes. (Burgess, in litt., 1958) Upper scale of abscissa, wind in cm/sec. Lower scale , number of mosquitoes/unit volume of air.

The maximum stimulatory height is therefore an unfortunate designation of a statistical concept. i.e. the probability that an insect flying at this height will orient is 1; the probability that an insect flying at any other height will orient is less than 1. Similar modifications should doubtless be made in the concept of the minimum height of flight.

Windspeed increases rapidly with height as Fig. 6 clearly shows, both upwind and downwind flight should be possible at any given moment. On the basis of optomotor theory one might predict both upwind and downwind flight to the left of the line MP in Fig.2 and Fig.3 even if windspeed did not vary with height. In order for an insect to "tell" if it is flying either upwind or downwind, the insect must not only obtain information about its airspeed and translational angular velocity, but also of its height above the background. Hocking (personal communication, unpublished) suggested that an insect may be able to "tell" its height above the background by resolving images of objects of "known" size in its environment. Hocking believes that his suggestion is substantiated by the ability of an insect to land successfully. However, an insect might be able to obtain the necessary information about its altitude to land successfully by virtue of the fact that the translational angular velocity becomes very large as the insect nears the ground. Hassenstein (1958a) (if I understand him correctly) has shown that an insect does not resolve images in the manner that the human eye does i.e. perceive a pattern. Apparently an insect derives all information about an object from flicker. Another possible way by which an insect might gain information about its height is by noting changes in angular movement when the insect "pitches" or "rolls." Wigglesworth (1939, p. 124) stated: "The simultaneous and equal illumination of corresponding points of the retina is probably the chief factor in the perception of distance."

Clearly, both upwind and downwind flight would not occur within any region of the diagram providing that an insect prefers upwind to downwind flight, and providing that the insect can estimate its height. And the field observations of Kennedy (1951) on locusts and those of Steiner (1953) on the beetle Geotrupes stercorarius L., seem to indicate that an insect can "tell" whether it is flying upwind or downwind.

It is interesting to note from Fig. 3 that downwind movement of northern Aedes mosquitoes such as Aedes punctor flying higher than about 235 cm. (ca. 8 ft.) and in winds greater than about 235 cm./sec. (ca. 5 m.p.h.) will occur. For windspeeds lower than about 235 cm./sec. some of the mosquitoes flying below 235 cm. will show steady upwind flight. The predicted behavior will be realized only if the background can be resolved. Doubtless the resultant displacement of a population of mosquitoes flying near the ground during total darkness would be more downwind than if the background were visible.

The situation is difficult to analyse during twilight hours because of the decreasing intensity of light. Orientation to cloud patterns or even to polarized light is possible. It is interesting to note that the polarization of skylight reaches a maximum about half an hour after sundown.

It would be of interest to know whether mosquitoes can detect their motion relative to the ground during hours of darkness. The only relevant field observations are those made with regard to swarming.

That the cessation of swarming is light-dependent has been suggested by several workers. Nielsen and Greve (1950) found that swarming of Aedes cantans Mg. ceased at 7 lux. Belkin et al (1951) observed swarming of Anopheles franciscans McCracken at light intensities of < 0.2 Weston units (ca. 2 lux).

More recently Provost (1958) found that males of Psorophora confinis ceased swarming at 0.02 lux. Moreover Provost found that on a moonlit night the illumination from the zenith never dropped below 0.025 lux; and swarming was prolonged an hour longer than on nights when the moon did not rise soon after sunset.

Since mosquitoes can perceive swarm markers on moonlit nights, one might expect that on such nights mosquitoes can also perceive their motion relative to the ground. One cannot draw any conclusions from observations on swarming about the ability of mosquitoes to navigate on dark nights since swarming presumably does not necessarily stop because the marker is no longer visible. The studies of Sato et al(1957b) on structural changes in the mosquito's compound eye during the process of dark adaptation may help to clarify this issue.

The structure of the mosquito eye has been studied by Sato (1950, 1953, 1957a, 1957b) in Anopheles hyrcanus sinensis Wiedemann, Culex pipiens var. pallens Coquillett and Aedes (Finlaya) japonicus Theobald. Sato and his coworkers found the respective facet numbers (95% reliability) for females of these species to be: 606-637, 503-560, 504-527. The eye was classified as the acone type and it forms only apposition images. Neither tracheal tapetum, tracheal sacs nor reflecting pigments were found in the eye. The internal arrangement of the ommatidium was found to vary with light intensity. In the dark adapted eye, the lens thickened proximally and the rhabdom migrated upward to touch the lens. Further the pupil of the ommatidium enlarged markedly because the iris pigment cells contracted and moved aside distally. Obviously in the dark adapted eye light from an unusually large solid angle can fall upon the rhabdom; if the insect is moving, light from a stationary point will fall

on the rhabdom for a longer period of time. Since intensity times duration is a constant (Dethier in Roeder, 1953) both luminosity discrimination and flicker perception will be enhanced in the dark adapted eye. At the same time visual acuity will decrease since the effective ommatidial angle is larger.

It seems reasonable to suppose that at the light intensity below which visual acuity is asymptotic to the logarithm of light intensity, flicker perception is impossible. According to Dethier (in Roeder, 1953, p. 508), however, the sigmoid curve relating visual acuity and log light intensity for the bee has a heel where log millilamberts equals -0.5. Below a light intensity of 0.7 millilamberts (ca. 7 lux), then, the visual acuity of the bee is effectively nil. Wigglesworth (1939) has reproduced a graph relating flicker perception to the logarithm of light intensity for the honey bee. However in this instance the heel of the curve is formed at log millilamberts equals -1.5. Hence flicker perception (or detection of movement) is negligible below .07 millilambert (ca. 0.7 lux). Flicker is perceived by the honey bee when the visual acuity is effectively nil!

If the perception of flicker is possible in light intensity below that required for effective resolution, than an insect although it could not hover above an object because of too low light intensities could still obtain information about its displacement relative to the ground. Sato et al (1957b) found that in Culex pipiens var. pallens Coquillett dark adaptation of the eye is about complete when the light intensity falls below 0.02 lux. One might expect, then, that the mosquito can perceive motion at even lower light intensities.

Apparently the orientation of mosquitoes to wind during hours of darkness has not been studied. However Larsen (1949) studied the migration of the noctuid Plusia gamma L., and found that at night the moths displacement was consistently with the wind.

Rees (1945) believed that moonlight exerts a profound influence on the movements of mosquitoes. According to Horsfall (1955), other workers also believe that the moon influences mosquito activity. Mosquitoes flying near the earth would certainly orient to wind during moonlight. The work of El-Ziady is doubtless relevant to Rees' hypothesis. El-Ziady (1957) studied the effect of moonlight on the vertical distribution of Diptera. From an analysis of traps catches taken at 5 ft. and 30 ft. levels above the ground she concluded that "there is a positive correlation between activity of insects and the moon. Insect population at this level (30 ft., W.K.) increases at F. M. (full moon W.K.) and decreases at N. M. (new moon W.K.), the reverse of what occurred at ground level...."

'The significance of these findings can be realized when considered in terms of problems of dispersal of insect pests if attracted to the moon. These fly to high levels of the atmosphere and are caught and transported by wind from one place to another. This point, however is being tested further on totally different climate and insects, to verify the validity of this phenomenon..."

How accurately the nocturnal movements of insects can be predicted from optomotor considerations is debatable. Nevertheless it is reasonable to expect more wind drift at night than during the day.

1.2.2. The Optomotor Theory and the Vertical Distribution of Dispersing Mosquitoes.

1.2.2.1. Implications on dispersion.

Numerous studies have been made on the distribution of insects in the atmosphere. Recently Johnson (1957) and Taylor (1958) found that the decrease with altitude of the number of insects per unit volume of air could be described by a mathematical relationship. These workers regard the aerial fauna as forming a continuous diffusion system.

A discussion of the vertical distribution of biting mosquitoes in forests can be found in Bates (1949). Snow and Pickard (1957) showed that the upward movement of mosquitoes was dependent on light intensity. This worker found that the mosquitoes remained high in the trees during the night and that the descent was initiated by the same light intensity (1 ft.-candle) as the ascent. More recently Love and Smith (1958) studied the vertical distribution of mosquitoes using mechanical sweeping devices at 3-, 6-, 15-, 25-, 40- and 50- foot levels. These workers found that: "The maximum numbers of Anopheles and Uranotaenia were collected at 6 feet, 51 percent of maximum at 3 feet, with a marked decrease at 15 feet continuing through higher elevations. The maximum numbers of Aedes and Psorophora were collected at 40 feet, with near maximum collections also taken at 25 feet and 3 feet. Fewer but still appreciable numbers were collected at 6 feet, 15 feet, and at the high 50-foot level. The greatest number of Culex was collected at 3 feet, the numbers decreasing at higher elevations, except for a secondary peak at 3 feet, with collections at other elevations varying only from 64 to 73 percent of this maximum."

Whether these observations can be extrapolated to a plain is highly questionable and for that reason the bearing of these observations on dispersion is also debatable.

The vertical distribution of mosquitoes over grassland was studied by de Zulueta (1950). His data indicate that the ratio of females caught in nets attached to a moving vehicle at 4.5 m. and 1.5 m. was ca. 1:6 for Culicine mosquitoes and ca. 1:10 for Anopheline mosquitoes. Horsfall (1955, p. 398) noted that three times as many female Psorophora discolor were collected in a whirling net trap at 1.2 m. as at 2.4 m. MacCreary (1941) operated two sets of two light traps at different locations. At each site one trap was about one hundred feet above the one near the ground. The percentages of total mosquitoes caught at the upper elevation were 3.3% and 8.8%. Burgess (in litt. 1958, 1959) trapped Aedes mosquitoes above pasture land at 5-, 25-, and 50- foot levels. He found that the density diminishes rapidly with height. Moreover his curves relating density with height are similar to those described by Johnson (1957). An approximate estimate based on these curves indicates that the ratio of the numbers present above the 10-foot level to those below 10 feet is 8:7 for his 1955 data, and 5:4 for his 1956 data. If the integral given by Johnson (1957) for Freeman's data for all insects is evaluated between the limits of 0 ft.-10 ft. and 10 ft.-277 ft. it is seen that only 5% of the airborne insect population is below 10 feet.

It was pointed out that mosquitoes such as Aedes punctor above about 235 cm. will either exhibit random orientation and their track will have a downwind component, or they will fly downwind.

According to the data obtained by Burgess, then, over half of the mosquito population will be wind-borne. Moreover Burgess found that the density profile may be established or destroyed rather quickly certainly within one hour. It is of great importance to know the rate of vertical exchange between insects near the earth's surface and those higher up. Atmospheric turbulence would affect the rate of turnover, however during the hours when mosquitoes are active, atmospheric turbulence is usually reduced by isothermal or inversion temperature lapse rate. The only physical factors which might cause an insect to cease flying are low temperature and the lack of energy. Hocking (1953) found that for mosquitoes: "Intermittent flight was obtained at temperatures down to 36°F." This worker found the flight endurance of Aedes punctor to be 12 hours. Further Hocking (1953) concluded:"For all species the dominant stimulus for flight was lack of tarsal contact. In mosquitoes air movement was next in importance...." Bassler (1957) has shown that the antennae bear sensory organs (Raumlag-sinnesorgan) which would enable the mosquito to maintain its normal flight altitude even in total darkness. If the mosquito were carried to high altitudes it would be excited to greater activity by the decrease in atmospheric pressure (Haufe, 1954). Since mosquitoes are rarely trapped at heights greater than a few hundred feet above the earth, the pressure changes experienced by mosquitoes may be much less than the pressure changes to which Haufe subjected mosquitoes.

The conclusion can be drawn from optomotor considerations and evidence from vertical distribution studies that mosquitoes can be carried by the wind. Those mosquitoes flying into the wind certainly will not travel as far as those flying with the wind.

Although the preferred airspeeds of mosquitoes are not well established the maximum airspeeds are known. According to the work of Hocking (1953) Aedes punctor-a fairly strong flier-could not make headway against a wind

greater than 235 cm./sec. This speed is no doubt much higher than that which a mosquito would fly against for a long period of time. The cruising speed of an insect will depend on its height above the background. Kennedy (1939) found this speed to be 17 cm./sec. for Aedes aegypti for a height less than 10 cm. Hocking (1953) found the cruising speed of Aedes punctor, 25 cm. above the background, was 78 cm./sec. Very low windspeeds, say below 150 cm./sec., were rarely observed in Edmonton during the time when this study was carried out. Nevertheless one cannot simply conclude that against-wind displacement of mosquitoes is negligible, because windspeed decreases very steeply as the earth's surface is approached (Fig.6). Hence by flying close to the earth a mosquito could make headway against the wind. Such headway would be very slow and doubtless changes in direction would occur because the wind is variable. The net displacement would then be small compared to the flight range as measured by Hocking (1953.)

From theoretical considerations, then, the displacement of active mosquitoes must show a very strong downwind component.

1.2.2.2. Factors influencing vertical distribution of mosquitoes.

(a) Environmental.

According to Glick (1957) the relative number of insects caught at 100 ft. at daybreak declines from 40 to 15 at sunrise. One reason for the increase in the population of the 100-foot level may be that insects lose visual contact with the ground during hours of darkness and fly higher above the earth. El-Ziady (1957) has suggested that the moon may attract insects to higher altitudes.

Freeman (1945) found that the number of insects in the air increases from 6-12 m.p.h. Glick (1957) reported the maximum number of insects in winds of 5-6 m.p.h.

According to Andrewartha and Birch (1954), Pittendrigh (1950) showed that the vertical distribution of mosquitoes in a forest is dependent on the relative humidity profile. When temperature inversions occur, the marked decrease of absolute humidity with height vanishes. When the atmosphere is dry, the humidity profile may effectively confine moisture sensitive insects to the earth's surface or perhaps to a certain height above the ground. However at night this barrier often vanishes, and insects can gain altitude.

According to Freeman (1945) an increase in temperature results in an increase in the air borne insect population until an optimum temperature is reached.

Nielsen and Nielsen (1958) found that Aedes caspius Pallas was confined to 100 cm. of the ground when the temperature was 10°C.; however Nielsen and Nielsen believe some other factor may also have been operative in this reduction of flight activity. Wellington (1944) observed that when temperature inversions exist male Culicine mosquitoes tend to rise above the layer of inversion. Burgess (in litt., 1958) found no similar influence of the temperature gradient in his data.

The influence of other environmental variables such as barometric pressure has not been demonstrated.

(b) Behavioral.

Clarke (1943) wrote with regard to Aedes vexans: "Observation at marshes during the period of emergence reveals that vexans rises from the marsh singly and continuously at dusk for a period of approximately one hour. They are observed to rise to a height of forty feet and fly with the wind." Nielsen (1958) observed that Aedes taeniorhynchus

takes off with wind during the initiation of its migratory flight. De Meillon (1934, as cited by Horsfall 1955, p. 230), observed that Anopheles gambiae when released rise to a height of 6 m. and then fly with the wind. Horsfall (1955, p. 24) states:"Most accounts have indicated that hordes of mosquitoes travelled more than 15 m. above the ground."

Whether the optomotor response is weak in all newly emerged mosquitoes as it may be in Aedes taeniorhynchus (Nielsen, 1958) is not known.

1.3. OTHER PECULIAR RESPONSES AFFECTING DISPERSION.

A form of behavior that would not only influence the vertical distribution of mosquitoes but also dispersion is the movement of mosquitoes along lines or borders (Jenkins and Hasset, 1951; Snow and Pickard, 1951.)

Horsfall (1955, p. 525) reported that a mass flight of Aedes vexans Meigen took place toward "the glowing skyline caused by suburban lights." Horsfall does not state the speed and direction of wind. Lindroth (1948) showed that some ground beetles Oodes gracilis Villa, Acupalpus consputus Dft. and A. dorsalis Fbr. fly to the west between 17 h and 19 h.

Horsfall (1955, p. 525) also reported that movements of mosquitoes may be restricted to the undergrowth: "Females were moving eastward in the undergrowth of a forest area during a sultry afternoon when no wind was blowing. The females flitted from one low plant to another,but always in the same general easterly direction. Such "creeping migration" seems to occur in Utah also (Rees, 1943). He, too, noted that females followed paths of low canopy vegetation. Within 2-5 days a flight had moved 8 km. in this case."

Were the movements of the mosquitoes confined to the undergrowth because of adverse temperature, humidity or light conditions, or is such

behavior the expression of an innate preference to movement within vegetation?

Hearle (1926) reported the movement of mosquitoes up the sides of mountains. Is this behavior skototaxis, or the attraction to prominent sections in the landscape, hypsotaxis? Schneider (1952) has shown that Chafers Melolontha sp. fly toward hills. Evans (1956) has data indicating that the percentage of a population of Chafers, Amphimallon majalis Razoumowsky, which go to a given object projecting above the horizon varies inversely as the square of the distance separating the Chafers and the object. Moreover Evans (personal communication, unpublished) believes that shape influences "attractancy" of an object.

MacCreary (1939) operated five light traps in Newark, Delaware. MacCreary found some traps collected more mosquitoes than others. He states:

"...The trap locations were examined with the thought of ascertaining any environmental differences that might exist. It was certainly not a matter of elevation, since the difference between that of the highest trap and the lowest was but 43 feet. Other visible conditions appeared to be nearly equal. Population density (of man, W.K.) appears to be the only explanation. The traps capturing the largest number of female mosquitoes were located in old and established sections of Newark. The other traps, although on opposite sides of town, were placed in comparatively new real estate developments with a much lower population density. Headlee (1936) has indicated that both Aedes vexans (Meig.) and Culex pipiens L. tend to migrate in the direction of great populations regardless of wind direction."

An alternate explanation for MacCreary's results is that initially the heavily populated part of the human community is not more attractive

than any other part of the community, however mosquitoes would tend to accumulate near this blood source. Unfortunately the evaluation of these hypotheses is not simple.

1.4. PASSIVE TRANSPORT.

Movements of mosquitoes other than those near the surface of the earth have also been reported. Smith et al.(1956) demonstrated with the use of marked mosquitoes that when a cool air mass moved across a semi-tropic area in California, vast numbers of mosquitoes were picked up and deposited 30-60 miles distant from the larval habitat. Smith (in litt., 1959) explained this transport as follows: "I do not have any air temperature data of the moving air but would assume it would not be much below 10° lower than the valley air.'

'I do not believe this mass could be considered as passing over in the nature of a frontal movement. Meteorological information indicated that it was a local movement drawn in from the coast over about 60 miles of low hot hills to fill a local barometric low and dissipated once it entered the valley. My belief is that the mosquitoes were not carried on this cool air or any local surface movement it set up but were stimulated by cool air and carried by thermal currents at higher altitudes..."

Horsfall (1954) described a mass transport of Aedes vexans in a cold front. Perhaps storm cells of the advancing air mass picked up the mosquitoes and carried them high into the air as is apparently also the case with the spruce bud worm moth Choristoneura fumiferana (Greenbank, 1956; Henson, 1951).

Wellington (1945, 1956) has pointed out that pressure changes associated with the passages of cold fronts "excite" some Diptera.

Haufe (1954) has shown that Aedes aegypti mosquitoes exhibit increased activity with pressure changes. However the pressure fluctuations produced by Haufe were different from those associated with a frontal passage or with a thunderstorm. Nevertheless Kennedy (1940) has shown that mosquitoes take flight when windspeeds are decreasing. It is therefore conceivable that mosquitoes, due partly to their own activity, could be carried by frontal systems.

1.5. SUPPRESSION OF SPONTANEOUS ACTIVITY BY EXTREME ENVIRONMENTAL CONDITIONS.

1.5.1. Introduction.

The dependence of the movement of mosquitoes on wind was pointed out. Moreover the conclusion was drawn that the displacement of a mosquito will have a strong downwind component. If the student of dispersion has a record of the daily march of environmental variables which influence an organism's movement, and further if he understands the exact manner in which these environmental variables and changes in them influence the displacement of the organism, he can predict the resultant displacement of a population.

I have considered wind to be the most important environmental variable which influences mosquito displacement. However the wind data alone will not enable one to predict the displacement of an organism because the environment often restricts or prevents activity (. .Larsen, 1943.) To predict the displacement of mosquitoes one must therefore consider the wind data from those hours when the mosquitoes were, or at least could have been, active.

The following environmental conditions are known to reduce the activity of mosquitoes: high windspeeds, low temperatures, low humidities, high light intensities.

1.5.2. The Influence of Windspeeds.

Reports in the literature on the influence of windspeed on mosquito activity are rather difficult to evaluate because windspeeds are rarely measured at the site of mosquito activity. The fact that the speed of wind is greatly influenced by vegetation and other obstructions has prevented both the theoretical and experimental physicist from arriving at an expression which can adequately describe in all situations the variation of windspeed and microstructure with height above the ground.

That windspeed increases with height above the ground is a well known phenomenon. Sutton (1953) has reviewed this subject. He states:

"In general terms it is clear that these results express the fact that the turbulent transfer of momentum from one level to another is either promoted or hindered by the prevailing density gradient. In conditions of superadiabatic lapse rate, the turbulence of the wind is at its highest level, and there is a free flow of momentum from the unretarded stream at the greater heights to replace that used up in overcoming the friction of the surface. In such conditions velocity tends to become nearly uniform with height, except in the immediate vicinity of the surface. When turbulence is being suppressed by an inversion, the vertical exchange of momentum is reduced and the velocity near the ground sinks to a much lower level, resulting in a more sharply curved velocity profile."

Clearly winds exhibit extremely complicated behavior even at exposed locations well away from any obstruction. Needless to say at any given time, there will be a wide variation in wind characteristics in a given habitat.

Hocking et al.(1950) suggest an explanation for reduction of activity with increasing windspeeds:

"The influence of windspeed both on flying and biting activity appears to be primarily a mechanical one; because controlled flight in the wind is difficult, biting is also difficult. However by increasing evaporation, higher windspeeds may also influence mosquitoes in the same way as high saturation deficiencies."

"Mechanical influence" doubtless refers not only to the influence of windspeed but also turbulence. It has been pointed out that temperature inversions which occur during the hours when mosquitoes are active tend to damp out turbulence. However the amount of turbulence is also related to the velocity of the wind. Hewson and Gill (1944) found that the amount of turbulence defined as the average amptitude of gusts varied almost linearly with windspeed. However the ratio of mean turbulence to velocity is not a constant: "It can be seen that the ratio increases with velocity up to about 5 m.p.h. After that the increase is more gradual, until at velocities above 12 m.p.h. the ratio is practically constant."

Judging from the study made by Hocking (1953) no mosquito could govern its track in a windspeed as high as 12 m.p.h. (ca. 550 cm./sec.) Insects flying near the earth surface could control their track since the windspeed would be much lower there. However if the wind is sufficiently gusty the eddies will extend to the surface of the earth. Under these conditions a mosquito cannot control its track. Wilson (personal communication) has assured the writer that 12 m.p.h. (ca. 550 cm./sec.) is a critical windspeed from a meteorological standpoint. At this windspeed the eddies penetrate to the surface as is evidenced by drifting of snow and soil.

Shemanchuk (1958) states that mosquito activity is reduced in windspeeds above 10 m.p.h. (ca. 470 cm./sec.) In this study the anemometer was at the site of the trap but considerably higher. Airflow around cylindrical traps is complicated and variable. Moreover in this study high winds were accompanied by adverse temperatures and humidity conditions.

In the studies made by Hocking et al (1950) and Curtis (1953), biting and landing rates were criteria of activity. Is it valid to extrapolate these data to predict spontaneous activity under identical meteorological conditions? Female mosquitoes are often observed to approach an observer during fairly high winds. In such instances the females fly just several inches above the ground. These mosquitoes may be stimulated by the observer and hence are not spontaneously active. From the graph published by E.B. Larsen (1948) one sees very little activity in winds greater than 3 Beaufort units (ca. 365-ca. 550 cm./sec.) Her criterion of activity was the number of mosquitoes feeding on the crowns of Tanacetum. Again feeding activity and flight activity are entirely different; however the fact that mosquitoes do not even feed when the turbulence extends into the vegetation suggests a dependence of activity on windspeed.

Horsfall (1955,p. 104) states that a number of workers found that in gentle winds Anopheles maculipennis exhibits "erratic" flight, however in strong wind, this species is grounded. Rudolfs (1923) observed little mosquito activity in winds over 6 m.p.h. (ca. 270 cm./sec.) Uvarov (1931) as cited by Wellington ( ) stated that mosquitoes are not active in wind over 8 m.p.h. (ca. 365 cm./sec.) Gordon and Page (1943) found that in winds over 12 m.p.h. (ca. 550 cm./sec.) mosquitoes were not taken in light traps. Afridi and Majid (1938) found that Culex fatigans would not take flight in wind above 10 m.p.h. (ca. 455 cm./sec.)

It is well known that aphids actively launch themselves into the air during winds of much larger speeds than an aphid's maximum airspeed. Whether mosquitoes would exhibit such behavior is open to question. Perhaps such "migratory" species as Aedes taeniorhynchus and Aedes sollicitans exhibit this type of behavior. Nielsen (1958) has observed Aedes taeniorhynchus taking off with the wind. Pearce (in litt., 1959) found that during low winds salt-marsh mosquitoes "move in hops of 50-500 yards." However during high windspeeds mosquitoes "tend to stay in flight and thus avoid our strip of insecticide."

Obviously the question of inhibition of activity by wind could be more satisfactorily discussed if more were known of the variation of "locomotory drive" with age. Even a knowledge of the sequence of various kinds of behavior would be helpful.

For the purpose of this study, the assumption was made that little spontaneous activity occurs in winds over 550 cm./sec. (ca. 12 m.p.h.)

1.5.3. The Influence of Temperature on Mosquito Flight Activity.

Mosquitoes do not exhibit spontaneous activity until the air temperature is much higher than that at which flight is possible. Hocking (1953) observed that mosquitoes on his flight mill exhibited flight activity at temperatures down to 36°F. Rudolfs (1923) found that the activity of Aedes sollicitans and Aedes cantator decreased below 60°F. and ceased almost entirely below 50°F. Mellanby (1940) concluded that the flight threshold of Aedes punctor is 10°C. (50°F.) in Lapland. Hocking et al (1950) recorded high biting rates at temperatures below 7°C. (45°F.) and also state: "Between temperatures of 50°F. and 80°F. there is no regular variation in attack; data beyond these limits are too meager for definite

conclusions but suggest that the intensity of attack falls off rapidly at both higher and lower temperatures." Curtis (1953) made a study similar to that of Hocking et al (1950). He states that "Activity ceased entirely at 36°F. and was negligible below 40°F."

The criterion of activity in the studies of Hocking et al and Curtis were rates of landing and biting. Of course one cannot assess the proportion of observed activity induced by the presence of the observer, and the proportion that was spontaneous. Shemanchuk (1958) has a relevant observation:" Female mosquitoes would land and bite in small numbers (1 to 1.6/min.) only immediately after the observer entered the sampling site. If the observer remained still for approximately 3-5 minutes, no bites would be recorded."

Nielsen and Greve (1950) in their study of swarming found a linear correlation between the time of evening ascent and temperature. According to their graph, the evening ascent would be at 1800 hr. with a temperature of ca. 70°F. and at 2100 hr. with a temperature of ca. 41°F. The temperatures in this instance were measured in the heather, and were as much as 9°C. (16.4°F.) lower than those recorded in the Stevenson screen. These workers also state that the duration of swarming is dependent on temperature: "It appears evident that swarming continues for a shorter time when it is cold and a longer time when it is warm. If the temperature is below 10°C. (50°F.) there will be no swarming at all." Moreover these authors state: " A few laboratory observations have been made on the temperature relationships of Culicids but all that appears to have been established is that they tend to avoid temperatures above 24°C. (75.2°F.) or below about 4-6°C. (39.2-42.8°F.) at which temperature they are to some extent immobilised." Wellington (1945) states that the minimum temperatures

at which male and female Culex mosquitoes cease to fly are 8.9°C.(48°F.) and 6.1°C. (43°F.) respectively. Nielsen and Nielsen (1958) however observed the topswarms of Culex at 8.6°C.-9.7°C. (47.5°F.-49.4°F.) Lewis (1933) made observations on Aedes aegypti,a species that does not occur in northern latitudes. He found that this species did not fly and walked about very slowly at 10°C.

It seems then that one can safely assume that mosquitoes exhibit little spontaneous flight activity below 50°F.

1.5.4. The Influence of Humidity on the Spontaneous Flight Activity of Mosquitoes.

The literature on the influence of humidity on activity is rather confusing, because some obervers express the amount of moisture in the air in terms of relative humidity and others as saturation deficit. Andrewartha and Birch (1954) state well the assumptions underlying both modes of expression, however their statements do not clarify the question insofar as mosquitoes are concerned. Cloudsley-Thompson (1956) states: "In insects which have a discrete epicuticular layer of wax and do not lose much water by evaporation except at temperatures above the critical transitional temperature of this wax layer, it is believed that the humidity receptors function hygroscopically rather than as evaporimeters..."

Since mosquitoes may have a discrete wax layer, relative humidity may be the mode of expression. However the manner in which humidity receptors work is probably not resolved so simply as Cloudsley-Thompson suggests.

Platt et al. (1957) have produced arguments supported by experimental data to the effect that Anopheles quadrimaculatus Say responds to changes in relative humidity and not to changes in saturation deficiency.

Platt et al.(1958)from a field study concluded that the spatial distribution of Aedes vexans is governed by relative humidity.

Larsen (1948) observed very little feeding activity when the relative humidity was below 80%. She expressed the opinion that activity follows the relative humidity curve. Hocking et al.(1950) found a marked reduction in biting activity at saturation deficiencies of 12 mm. Hg or more. Curtis (1953) did not find a consistent variation of biting activity with saturation deficiency. Shemanchuk (1958) found that the size of trap catches kept pace with the relative humidity. High humidities apparently never suppress activity, although Thompson (1938) found that Culex fatigans avoids high humidities. Rudolfs (1923) also believed that extremely high relative humidities are detrimental to mosquito activity. However Nielsen and Greve (1950) and Bertram and McGregor (1956) found that mosquitoes remain active during rain. However Roberts and O'Sullivan (1948) found that during heavy rain, activity ceased. Platt et al.(1951, 1958) maintain that Anopheles quadrimaculatus Say and Aedes vexans prefer a relative humidity between 70% and 80%. This range is in close agreement to that given by Rudolfs (1923).

For purposes of this study it is assumed that spontaneous activity is very light for relative humidities below 30%.

1.5.5. The Influence of Light Intensity on Mosquito Activity.

A positive correlation between cloudiness and mosquito attack was reported by Hunter (1910.) Hocking et al. (1950) report a well marked positive correlation on the tundra but less so in the forest. Curtis (1953) stated that:"On several occasions an increase in activity occurred concurrently with a reduction in light intensity, when all other factors were

relatively stable...However no clear cut example of the converse was obtained."

E. B. Larsen (1948) suggested that "activity shows evidence for light control, there is a dawn dusk activity peak all seasons." Nielsen and Greve (1950) found no correlation between light intensity and the beginning of the ascent of swarms; but with regard to swarming: "The evening swarms appeared to be formed in response to decreasing light intensity and to disperse at a light intensity of 7 lux..." These workers also report that "we have on occasions noticed the daytime swarms well outside the normal swarming times and apparently resulting from a fall in light intensity associated with approaching rain."

In this analysis the amount of cloudiness is employed to support conclusions drawn on the basis of the other environmental variables. The amount of cloudiness influences the temperature within the foliage, the development of inversions, of valley winds, and the windspeed within the river valley. Obviously, then ordinary weather data needs refinement when extrapolated to predict readings in a particular habitat.

2. SPECIAL SECTION- THE EDMONTON PROBLEM

2.1. THE PROBLEM: HISTORICAL.

Although no quantitative data were obtained regarding the density of adult mosquitoes, the Community Affairs Committee of the Edmonton Chamber of Commerce considered the mosquitoes in the Edmonton area to be a great threat to human comfort. This committee addressed itself to the problem of mosquito reduction. At a meeting March 2, 1953, advice on the efficacy of control measures and on organizational machinery necessary for this task, was given by J. H. Brown of the Provincial Dept. of Health and by B. Hocking of the University of Alberta. The task of mosquito reduction was assigned to the City Parks Dept. then supervised by Mr. A. C. Patterson. In 1955 mosquito control was placed under the supervision of Mr. J. Wright who later succeeded Mr. A. C. Patterson as superintendent of the Parks Dept.

Collections and determinations of mosquitoes in the Edmonton area had been made by Professor E. H. Strickland and other entomologists who followed this pioneer to Edmonton. At the time that the Parks Dept. undertook mosquito reduction, thanks to the work of these entomologists, about 30 species of mosquitoes were thought to be present in the Edmonton area. Since that time Dr. B. Hocking of the University of Alberta extended the knowledge of species present, their temporal distribution, and their relative abundance.

Larviciding by aircraft and by crews of men on foot has been the main control measure used. This larviciding campaign has been carried out each year over an area of radius 8 miles with the corner of 101 St. and Jasper

Avenue as the center. Neighboring municipal districts co-operated in this program by distributing "Tossits" in pools. The Town of Jasper Place and the Town of Beverly also supported the control program.

Adult control measures have been used only to a very limited extent. According to the 1953 report on mosquito control by A. C. Patterson, adults were controlled on limited areas such as the golf courses, playgrounds, Renfrew Park and Clarke Stadium. The surfaces of these areas was sprayed with a D D T and chlordane mixture. According to the report by Patterson the results of this measure were not encouraging: "We get a very good kill of mosquitoes..but more mosquitoes move in fairly quickly and do not seem to be adversely affected by the spray. Sometimes the control does not last any longer than about 12 hours."

Since the beginning of mosquito control in 1953, most of the pools within the City have been drained. Despite this reduction in breeding areas and annual application of insecticides to those which remain, large populations of mosquitoes appeared within the river valley which lies athwart the City. The Parks Department in 1956 decided that the origin of these mosquitoes should be investigated. A research grant was made available to a University student to study this problem.

2.2. THE TERRAIN.

The City of Edmonton lies 2200 feet above sea level on a flat plain gently sloping to the northeast. According to Moss (1955) Edmonton (53°33' lat., 113° 30' long.) is established on the black soil of the Boreal-Parkland Transition zone.

Edmonton straddles the North Sask. River which meanders across the plain from the southwest to the northeast. Several creeks flow into the North Saskatchewan River. On the south side of the river, White Mud,

Mill and Fulton Creeks are the most prominent. On the north side of the river several very short ravines join the river. The region from the northwest to the southwest from the city is covered more or less by swamps and lakes. The remainder of the region surrounding the city is covered with much less water. Most of the trees have been cleared from the land. Wooded areas exist only where the water table is too high to permit cultivation. In the immediate vicinity of the city, no large wooded areas remain. However large wooded areas still remain several miles west and northwest of the city.

Within the city, the wooded areas are almost completely confined to the river valley and adjoining ravines. Generally aspen poplar are the dominant trees, however in the deeper ravines and shaded areas of the river valley spruce predominate. The undergrowth is typical of poplar associations. Willow (Salix bebbiana) and dogwood (Cornus stolonifera) constitute a tall substratum. Roses (Rosa sp.), raspberries (Rubus sp.) and honeysuckle (Lonicera sp.)are predominant in the shrub stratum. Vicia americana, reed-bent grass (Calamagrotis sp.), Aster sp., bedstraw (Galium sp.), lungwort (Mertensia sp.), willow-herb (Epilobium sp.) and grasses (Agropyron sp.) are some of the herbs found. Along the river valley saskatoon and chokecherry abound. On the bogs, peat forming moss (Sphagnum sp.) and Labrador tea (Ledum) are found.

2.3. PROCEDURE.

Since the movements of mosquitoes in an area of about 100 sq. mi. were of interest, and since only one person was available for the work, it seemed apparent that the best procedure would consist simply of field observation.

An attempt was made to define the areas in which larvae were being produced. The area was surveyed from the air and from the ground. Larval samples were drawn both within and outside of the city limits. Screen rearing cages of the type described by Twinn (1950) were set up in some pools several miles east and west of the city. Samples of adult mosquitoes were drawn throughout the summer in as many places as possible. Enquiries about biting activities of mosquitoes were also made. Two visual attractant mosquito traps were operated, one on the Mayfair Golf Course and one on Summit Drive.

Meteorological data was recorded as follows:

	Wind	R. H.	Temp.	Cloudiness
Mayfair Golf Course (E1)	Yes	Yes	Yes	
Summit Drive (E5)		Yes	Yes	
Highlands Golf Course		Yes	Yes	
Two miles west of Edmonton (C)		Yes	Yes	
Mouth of Mackinnon Ravine (M)		Yes	Yes	
Airport	Yes	Yes	Yes	Yes

2.4. METEOROLOGICAL OBSERVATIONS.

(a) Description of sites.

The hygrothermograph on the Mayfair Golf Course was placed to the southeast of a small clump of poplars. On a knoll about one hundred yards to the east of the hygrothermograph, the anemometer was mounted twenty feet above the ground.

In a small clearing on the floor of MacKinnon Ravine, a hygrothermograph was placed.

On the plain just 50 paces south of MacKinnon Ravine, a third hygrograph was located with small trees to the west and large spruce to the north. About twenty paces to the south lay the pavement of the street.

(b) Results.

The thermohygrograph traces for two weeks have been traced onto a single chart. It should be noted that all of the thermohygrographs were run together in the laboratory before being set out. Readings of the instruments were checked with a psychrometer throughout the season.

On clear days the temperature record on the plain above MacKinnon Ravine had a higher minimum temperature than either recorded on the floor of MacKinnon Ravine or on the Mayfair Golf Course. (See Pl. XXI; Pl. XXII) Further the rate of cooling in the late afternoon was much slower than in the valley. The MacKinnon Ravine temperature trace shows the highest maximum in the afternoon. On the other hand MacKinnon Ravine remains cold for the longer periods each day than the other two sites.

The curves of relative humidity indicate that the relative humidity of MacKinnon Ravine is higher for longer periods of time and less subject to fluctuations than either the relative humidity at the Mayfair Golf Course or on the plain above MacKinnon Ravine.

The relative humidity on the Mayfair Golf Course is also generally higher and less variable than on the plain near MacKinnon Ravine.

The differences in relative humidity are due not only to differences in temperature, but in vapour pressure (Pl. IV). On more or less clear days, the maximum temperature was recorded in MacKinnon Ravine. In the early afternoons, the relative humidities fell to about the same value at all sites.

During the day a fairly strong breeze was observed to blow up MacKinnon Ravine. The maximum temperature was observed in the ravine probably because the hot air from the stony river margin flowed up the ravine.

Observations made an hour or two after sunrise indicated that on the sides of the river valley exposed to the sun, the air rose vertically. However air flowed down the shaded sides. It is doubtful however that a pattern of circulation is ever completely established in the manner depicted in the diagrams of Wagner (1938) or those of Hewson and Gill (1944). This suspected deviation from the classical concept of air circulation in valleys is doubtless due to the fact that the over all wind breaks through into such a shallow valley.

No up-valley winds such as those so well described by Defant (1949, 1951) were observed in this valley presumably because of the valley is flat and shallow.

Large "drops" of fog were observed to proceed down a number of the ravines. On May 22 rain fell around 18:30. At 21:00 MacKinnon Ravine was visited and fog was observed to flow down the ravine at an estimated speed of about 3 m. p. h. Using bits of cotton-wool the movement of air over the edge and down the sides of the ravine was studied. Observations of this nature were made on many calm nights when fog was not formed. Drainage of cold air down these ravines was observed to be a constant feature during the evenings and nights.

On July 9, 1958, hail fell and on melting, fog formed near the ground. Every depression was filled with fog. Fog drained down every ravine and hollow leading to the river valley. The fog also proceeded down the river valley. Even though the layer of fog within the river valley was rather shallow, observations on smoke rising from stacks within the valley indicated that all of the air up to the rim of the valley was flowing along the valley. Smoke rising below the rim of the valley was deflected in the

down valley direction whereas smoke rising above the rim of the valley moved northward. At this time, the wind at the airport was south at 6 m.p.h.

The fog flowing along the river valley did not everywhere follow the river but cut across the Mayfair Golf Course. Just south of this golf course, the fog rose high along the eastern side of the valley. It was suspected that air flow from ravines across the valley deflected the main stream of air flowing down the valley. However this hypothesis has not been evaluated. A down valley wind has been observed on a number of occasions when the wind was blowing across the valley. This phenomenon is not well borne out by the scatter diagrams of wind in the valley and at the airport for a given direction recorded at the airport.

Originally it was suspected that the valley might exert a steering effect on the over all wind. If a marked steering effect existed the winds blowing in a direction nearly coinciding with the direction of the valley would be expected to show a close one-to-one correlation. To be explicit, the windspeed measured at the airport should be very nearly the same as that measured in the valley. If the wind direction is across the valley, on the other hand, one should expect a lower windspeed in the valley than at the airport. It was thought that the "steering effect" should be especially evident during periods when the valley received no insolation. This phenomenon is not well borne out by the scatter diagrams either.

It can however be seen that during the night (for low windspeeds as measured at the airport) the windspeeds in the valley are generally lower than those at the airport. During high windspeeds, the speeds measured at both sites approach one another. For windspeeds above 20 m.p.h. the

windspeed measured in the valley is often higher than at the airport, presumably due to turbulence created by the valley.

During daylight hours, the speeds of wind measured at the two sites are more nearly the same. This is doubtless so because the air is more buoyant when lapse rates are superadiabatic. During cloudy periods however windspeeds in the valley are much lower than on the plain. As is the case at night, with high windspeeds these differences vanish. These facts are well illustrated in the scatter diagrams (Pl. IV to XX), and also in the charts showing the march of windspeeds throughout the day (Pl. I, Pl. II, Pl. III).

2.5. THE LARVAL SOURCE REGIONS.

Most of the pools were to the north, northwest, west and southwest of the city. Few pools were found in other regions. Very few pools were found within the city. Many shallow pools dried up rapidly because of lack of precipitation, high winds and exceptionally low humidities.

The area in which larvae were killed is shown on the map of larval distribution (Pl. XXIII).

All of the species were found together in most of the pools as the map of larval distribution indicates. However Aedes flavescens was found in largest numbers in grassy pools.

Most of the pools were shallow and of a temporary nature formed from the spring run-off. Since the reflectivity of pools was low, the water temperatures exhibited a fairly wide daily fluctuation. Unfortunately reliable temperature readings were not obtained from the thermograph. During April ice was often formed on the pools. Although larvae were found as early as April 8th very little development occurred before the third week in April.

2.6. OBSERVATIONS ON DATES OF ADULT EMERGENCE.

In order to get an approximate estimation of the time when adults emerged rearing cages of the type described by Twinn (1950) were set up in two pools. One pool, two miles east of the city limits, was overgrown by willow and poplar. The other pool was a grassy slough two miles west of the city limits. Adults were removed as often as possible.

It is seen from Table 3 that the peak emergence of Aedes cataphylla must have occurred prior to May 19 but not sooner than May 14. Further, the peak emergence of Aedes fitchii occurred prior to May 30 but not earlier than May 28.(Table 3).

2.7. OBSERVATIONS ON ADULTS.

Observations were made at as many sites as possible within one night. The duration of spontaneous activity on any given evening was rather brief. On warm calm nights, mosquitoes left their resting places around 18:30 hrs. The sun set at about 20:30 hrs., and activity usually ceased within an hour thereafter. Subjective estimates of the relative densities of mosquito populations at two different places and at two different times were difficult to make. In order to offset the influence of varying amounts of spontaneous activity on these subjective estimates, the vegetation was disturbed. By this procedure, a subjective estimate of the density of mosquitoes could be made.

Aedes cataphylla was often observed to swarm over small bushes, curbs of sidewalks, fence rails and dark patches of earth. On several occasions swarming was observed over mowed grass on the golf courses. In these instances, no swarm marker was apparent to the observer other

Table 3. Emergence of Adults. Spring 1958.

Date	Aedes Species	Number of Adults in Cage West of City ♀	Number of Adults in Cage West of City ♂	Number of Adults in Cage East of City ♀	Number of Adults in Cage East of City ♂
May 13					
May 19	implicatus	6	3		
	cataphylla		5	14	3
	compestris		1		
	impiger		1		
May 21	cataphylla				1
May 27	excrucians	1			
	fitchii	2			
May 30	fitchii			22	
	increpitus			7	
	stimulans			2	
	excrucians			11	
	campestris				
	communis				2
	canadensis				2
June 4	fitchii	10			
	excrucians	3	1		
	stimulans	1			
	campestris		3		
	communis		1		
June 7	fitchii			10	
	flavescens			3	
	communis				3
	canadensis				1
June 17	flavescens			1	
	fitchii			3	
	cataphylla			1	
	implicatus			1	
	cinereus			1	
	increpitus			1	

than perhaps the marks left by the mower.

Many of the swarms extended from 1½ ft. to about 10 ft. above the ground. In small clearings, the swarms were observed to be formed higher above the ground than in the open. Mating was often observed in the swarms. At 14:30 hrs. on May 18, a very small swarm of Aedes cataphylla was observed. The wind was light, large cumulus clouds obscured the sun, the temperature was 65°F. but the relative humidity was only 25%. Large swarms of Aedes cataphylla were often observed near the visual attractant mosquito traps. However the catches at such times were extremely low.

The first adult mosquito was taken on April 12 by Sheila Stewart, a student at the University of Alberta. This was a specimen of Anopheles earlei Vargas. The presence of overwintering mosquitoes was occasionally observed thereafter.

A brief summary of observations made until the end of June is presented below. E1 and E5 are visual attractant mosquito traps on the Mayfair Golf Course and Summit Drive respectively.

DATE	OBSERVATIONS
May 10	Buds burst on poplars in river valley. ♀ A. cataphylla Dyar seen - one at E5, three at a pool two miles east of city limits.
May 11	3 ♀ A. cataphylla Dyar taken in trap E5 - no other mosquitoes seen in city or within two miles east of eastern city limits.
May 12	No adults observed in valley, adjoining ravines, wooded regions two miles east of eastern city limits. At latter locality pupae were present in pools. E5: 1 ♀ A. cataphylla: 1900 h.
May 13	No mosquitoes encountered in valley and ravines before sunset. None encountered after sunset in area west and northwest to Big Lake. Many pupae in Big Lake region.
May 14	No mosquitoes encountered on golf courses. E5: 1 ♀ A. cataphylla: 1700 h.; 1 ♂ A. cataphylla: 2300 h.
May 15	E5: A. cataphylla: 3 ♀♀ : 1900 h.; 3 ♀♀ : 2100 h.; 1 ♂, 1 ♀ : 2200 h.; 2 ♀♀ : 2300 h. 2000 h. - quite heavy biting along MacKinnon Ravine. None elsewhere. Identified as A. cataphylla and A. pionips.
May 16	No adults encountered on golf courses or at trap sites. E5: C. alaskaensis: 1 ♀ : 0100 h.; A. cataphylla: 2 ♀♀: 0100 h.; 1 ♀ : 2300 h.; A. impiger: 1 ♂ : 0800 h. E1: A. cataphylla: 1 ♀ : 0100 h.-1700 h.
May 17	No mosquitoes encountered during day above MacKinnon Ravine and on golf courses. Large swarms and mating observed at E1 at 2000 h. (Temp. 55; R. H. 43%; slight breeze.) E1: C. alaskaensis: 1 ♀ : 0100 h.-1400 h.; A. cataphylla: 2 ♀♀ : 1500 h.; 1 ♀ : 1700 h.-2000 h.; 2 ♀♀ : 2200 h. E5: A. cataphylla: 1 ♀ : 0100 h.; 2 ♀♀ : 0400 h.; 9 ♀♀: 0600 h.; 1 ♀ : 0700 h.; 3 ♂♂, 17 ♀♀ : 0800 h.-1900 h.; 6 ♀♀, 1 ♂ : 2000 h.-0900 h. May 18; A. pionips: 1 ♀ : 0600 h.
May 18	Many biting mosquitoes at White Mud Creek, 1400 h. Swarms seen at 15:45 h. - A. cataphylla. E5: A. cataphylla: 1 ♀ : 1000 h.; 42 ♀♀, 14 ♂♂ : 1100 h.-2100 h.; C. alaskaensis: 1 ♀ : 2200 h. E1: A. cataphylla: 1 ♀.
May 19	No adults encountered either east or west of city. Resident at MacKinnon Ravine reported swarming at 1200 h. E5: A. cataphylla: 1 ♀ : 1000 h.; 1 ♀ : 1400 h.; 2 ♀♀ : 1600 h. 1 ♀ : 1700 h.; 1 ♀ : 2100 h.; (?) 1 ♂ : 0700 h. E1: A. cataphylla: 1 ♀ : 1800 h. Much emergence in all rearing cages. Sweeping in MacKinnon Ravine yielded only 1 ♀ A. cataphylla other than this.

DATE	OBSERVATIONS
May 20	Mosquitoes active at MacKinnon Ravine around 0900 h. - residents complain. No activity during day. Evening much swarming (A. cataphylla) in river valley and along adjoining ravines, for several miles southwest of city. No activity observed in wooded regions 1 mi. south of the river valley. E5: A. cataphylla: 4 ♀♀, 1 ♂ : 2200 h.; 6 ♀♀, 4 ♂♂: 2300 h.; A. implicatus: 2 ♀♀: 2200 h. E1: A. cataphylla: 1 ♀ : 1800 h.
May 21	In A. M., much biting at White Mud Creek. Removed only 1 ♂ from cages. E5: A. cataphylla: 1♂ : 0100 h.
May 22	P. M.: large swarms above almost every bush and tree along river valley.Biting in MacKinnon Ravine. E5: A. cataphylla: 4 ♀♀, 3 ♂♂ : 1200h.-1900 h.; 1 ♀ : 2000 h.
May 23	Riverside Golf Course: 19:30 h.-20:30 h.: very difficult to catch a good sample - 2 observers: A. pionips: 11 ♀♀; A. implicatus: 6 ♀♀; A. intrudens: 5 ♀♀; A. cataphylla: 2 ♀♀, 14 ♂♂ (swarm); A. sticticus: 1 ♀. Highlands Golf Course: 2100 h. - diffuse swarm A. cataphylla . Made numerous enquiries at residences and at club house - only one golfer had seen a diffuse swarm - no biting reported. E5: A. cataphylla: 1 ♀ : 0600 h.
May 24	No mosquitoes encountered in afternoon. Evening - no observations made. E5: A. cataphylla: 4 ♀♀: 1900 h., 3 ♀♀: 2000 h.
May 25	Early P. M. at mouth of MacKinnon Ravine collected: A. cataphylla: 14 ♀♀; A. implicatus: 5 ♀♀; A. intrudens: 4 ♀♀; A. stimulans: 2 ♀♀. Late P.M. swarming all along MacKinnon Ravine: A. cataphylla: ♀♀, ♂♂; A. implicatus: ♀♀; A. impiger:♀♀, ♂♂; A. intrudens: ♀♀; A. communis: ♂♂. E5: A. cataphylla: 4 ♀♀, 5 ♂♂: 1900h.-2100 h. A. fitchii: 2 ♂♂ : 1900 h. - 2100 h.
May 26	Visited all golf courses, mouth of MacKinnon Ravine and wooded area 2 miles northwest of city limits during A. M. Few mosquitoes active. P.M.: some biting above river. Very few mosquitoes at site of proposed zoo. E5: A. fitchii: 1 ♀ : 1900 h.; 1 ♀ : 2200 h.
May 27	19:30 P.M.: mosquitoes attacking cattle at White Mud: A. cataphylla: 17 ♀♀; A. implicatus: 1 ♀; A. intrudens: 1 ♀. Many very large swarms A. cataphylla all along White Mud Creek. E5: A. cataphylla: 2 ♀♀: 0100 h.-1200 h. A. stimulans: 1 ♀ : 2000 h.; 2 ♀♀ : 2100 h.; 3 ♀♀: 2200 h.

DATE	OBSERVATIONS
	A. implicatus: 1 ♀ : 2200 h. Winterburn rearing cage: A. fitchii: 1 ♀; A. excrucians: 2 ♀♀.
May 28	A. M. on White Mud-Black Mud junction: A. punctor: 1 ♀; A. cataphylla: 2 ♀♀; A. fitchii: 2 ♀♀; A. stimulans: 1 ♂. P. M.: Riverside Golf Course: numerous biting A. fitchii ♀♀. E1: A. fitchii (?) 1 ♂ : 0100 h.-1000 h. Attendants on Mayfair say mosquitoes not troublesome.
May 29	No mosquitoes encountered on Mayfair Golf Course or along MacKinnon Ravine. E5: A. cataphylla (?): 1 ♀ : 2100h.-2200 h.
May 30	Much emergence in rearing cages east of city: A. fitchii: 22 ♀♀; A. campestris: 1 ♂; A. increpitus: 7 ♀♀; A. communis: 2 ♂♂; A. stimulans: 2 ♀♀; A. canadensis: 1 ♂. Only few larvae and pupae remaining. E5: Culiseta sp.: 1 ♀ : 0100 h. E1: A. fitchii: 1 ♀ : 0700 h.-1200 h.; A. implicatus: 1 ♀: 1900 h.
May 31	No mosquitoes in evidence on Mayfair Golf Course or along MacKinnon Ravine during forenoon and afternoon. E5: A. implicatus: 1 ♀ : 1900 h.; A. fitchii: 1 ♀ : 2300 h.
June 1	No mosquitoes encountered on Mayfair Golf Course or along MacKinnon Ravine during forenoon and afternoon. E1: A. fitchii: 1 ♂: 0200 h.; 1 ♀ : 0900 h.-2100 h.
June 2	In A.M.: Highlands Golf Course - no mosquitoes seen. Mayfair Golf Course - no mosquitoes seen. Mouth of MacKinnon Ravine - very many fiercely biting mosquitoes. Wooded area 2 miles northwest of city - no mosquitoes seen. In P.M.: White Mud Creek - diffuse swarm of A. cataphylla; further west and south along river - no swarms seen. E5: A. fitchii: 1 ♀, 2 ♂♂ : 2100 h. E1: A. fitchii: 5 ♀♀, 4 ♂♂: 0100 h.-0900 h.; A. stimulans : 1 ♂ : 0100 h.-0900 h.
June 3	A. M. : no biting mosquitoes encountered on Mayfair Golf Course; mouth of MacKinnon Ravine: A. fitchii: 11 ♀♀; A. implicatus: 1 ♀. E5: (did not operate between 1500 h.-2000 h.) A. fitchii: 1 ♀, 7 ♂♂ : 2100 h.; 1 ♂ : 2200 h.; 2 ♂♂: 2200 h.; A. stimulans: 1 ♂ : 2100 h.; C. alaskaensis: 1 ♀ : 2100 h. E1: A. stimulans: 1 ♀ : 0900 h.-2300 h.; A. excrucians: 1 ♂ : 2400 h.
June 4	Many mosquitoes resting in MacKinnon Ravine. Some on Municipal Golf Course although no golfers complained: collected A. fitchii: 10 ♀♀, 3 ♂♂. Highlands Golf Course: few mosquitoes; difficult to collect: A. fitchii (?): 15 ♀♀; A. fitchii: 2 ♀♀, 6 ♂♂; A. stimulans: 1 ♂; A. excrucians: 1 ♂; A. campestris: 11 ♂♂.

DATE	OBSERVATIONS
	St. Albert: at 1900 h., mosquitoes rather inactive - A. flavescens: 2 ♀♀, 1 ♂; A. fitchii: 5 ♀♀; A. fitchii (?): 10 ♀♀; A. excrucians: 1 ♀; A. stimulans: 1 ♀; A. cataphylla (?): 1 ♀; A. viparius: 1 ♂. E5: A. fitchii: 2 ♀♀: 0200 h.; 1 ♀ : 2100 h.; 1 ♀ : 2200 h.; 1 ♂ : 2300 h.; C. inornata: 1 ♀ : 0200 h.
June 5	A. M.:Little activity near trap sites or west of city. Winterburn Swamp: A. fitchii: 4 ♀♀; A. stimulans: 5 ♀♀; A. excrucians: 2 ♀♀; A. implicatus: 1 ♀. E5: A. fitchii: 1 ♀, 1 ♂:0900 h.-1000 h.; 1 ♀ : 2300 h.; 3 ♂♂ : 2400 h.; A. stimulans: 6 ♂♂ : 0900 h.-1000 h.; 3 ♂♂ : 2300 h. E 1: A. stimulans: 1 ♂: 0100 h.-0800 h.; 3 ♀♀, 1 ♂ : 1800 h.-2200 h.; A. pionips: 1 ♀ : 1800 h.-2200 h.; A. excrucians: 1 ♂ : 1800 h.-2200 h.; A. fitchii: 12 ♂♂: 1800 h.-2200 h.
June 6	Very little activity evident on Mayfair Golf Course or along MacKinnon Ravine during forenoon. E1: A. fitchii: 1 ♂ : 1000 h.; 1 ♀ : 2300 h.; 5 ♂♂ : 2400 h.
June 7	Little activity at trap sites in forenoon. At rearing cages two miles east of city, numerous mosquitoes were resting in vegetation. Rearing cages: A. fitchii: 10 ♀♀; A. flavescens: 4 ♀♀; A. canadensis: 1 ♂; A. communis: 2 ♂♂. E5: C. inornata: 1 ♀ : 0300 h.; A. fitchii: 1 ♀ : 1600 h.; 1 ♀ : 1900 h.; 1 ♀ : 2000 h.; A. stimulans: 1 ♀ : 1900 h.; A. communis: 1 ♂ : 2300 h. E1: A. fitchii: 1 ♀ : 1600 h.-2300 h.; A. implicatus: 1 ♀ : 1600 h.-2300 h.
June 8	Children along MacKinnon Ravine report heavy biting. However, during afternoon no mosquitoes were encountered. E5: A. stimulans: 1 ♀ : 1900 h.; A. fitchii: 1 ♀ : 1200 h.; 2 ♀♀, 1 ♂ : 2100 h.; 2 ♀♀ : 2400 h. E1: A. fitchii: 3 ♀♀ : 1000 h.-1800 h.; 1 ♀ : 1900 h.; 7 ♀♀ : 2000 h.; 1 ♀ : 2200 h.; A. stimulans: 2 ♀♀ : 2000 h.
June 9	In A. M.: Mosquitoes not active on Highlands Golf Course, Mayfair Golf Course and wooded area 2 miles northwest of city. Mosquitoes in evidence in MacKinnon Ravine. E5: A. fitchii: 1 ♀ : 0100 h.; 1 ♀ : 0300 h.; 1 ♀ : 0400 h.; A. excrucians: 1 ♀ : 0100 h.; A. flavescens: 1 ♀ : 0300 h.; C. inornata: 1 ♀ : 0200 h. E1: A. fitchii: 1 ♀ : 0900 h.
June 10	A. M. : Mosquitoes not evident. Evening: collected in a cowshed at White Mud: A. fitchii: 8 ♀♀; A. impiger: 1 ♀; collected in horse pasture southwest of White Mud, near river. Mosquitoes bite reluctantly. Collected - A. fitchii: 10 ♀♀;

DATE	OBSERVATIONS
	A. implicatus: 7 ♀♀; A. trichurus: 1 ♀; A. cataphylla: 3 ♀♀; A. communis: 1 ♂; A. fitchii (?): 2 ♀♀. Lady reports mosquitoes are "very bad." At Mill Creek, difficult to draw a sample - A. fitchii: 8 ♀♀; A. excrucians: 4 ♀♀. E1: A. implicatus: 1 ♀ : 0100 h.-0900 h.; A. fitchii (?): 1 ♀ : 0100 h.-0900 h.; A. fitchii: 2 ♀♀ : 2000 h.; 1 ♀ : 2300 h.; C. inornata: 1 ♀ : 2000 h.
June 11	A. M.: No mosquitoes active at trap sites. Late P.M.: Mosquitoes resting in bushes on Mayfair Golf Course. A. fitchii: 16 ♀♀; A. excrucians: 9 ♀♀; A. flavescens: 7 ♀♀; A. fitchii (?): 10 ♀♀. E5: A. flavescens: 1 ♀ : 2300 h.; 1 ♀ ; 2400 h.; A. fitchii: 1 ♀ : 2200 h.; 1 ♂, 1 ♀ : 2300 h. E1: A. fitchii: 1 ♀ : 0100 h.-2100 h.; A. flavescens: 1 ♀ : 0100 h.-2100 h.
June 12	A. M.: Heavy biting at bottom of MacKinnon Ravine. None at location of proposed zoo. E5: A. fitchii: 1 ♂ : 0300 h. E1: A. flavescens: 1 ♀ : 0100 h.-1000 h.
June 13	E5: C. tarsalis: 1 ♀ : 0100 h.-2100 h.; A. flavescens: 1 ♀ : 0100 h.-2100 h.; A. excrucians: 1 ♀ : 0100 h.-2100 h. E1: A. fitchii: 1 ♂ : 2100 h.; A. flavescens: 1 ♀ : 2100 h.
June 14	E5: A. fitchii: 1 ♀ : 2200 h.; A. stimulans: 1 ♂ : 2100 h.; 1 ♂ : 2200 h.
June 15	E5: A. flavescens: 1 ♀ : 2200 h.; 1 ♀ : 2300 h.; A. fitchii: 1 ♂ : 2300 h.; A. stimulans: 9 ♀♀: 2100 h.; 22 ♀♀ : 2200 h.
June 16	A. M. : No apparent activity at any meteorological sites. E5: A. cataphylla: 1 ♀ : 0300 h.; A. fitchii: 2 ♀♀ : 2400 h.; C. inornata: 1 ♀; A. stimulans: 4 ♀♀ : 2300 h. E1: A. stimulans: 1 ♀ : 0900 h.
June 17	E5: A. stimulans: 1 ♂ : 0100 h.-0900 h.; 2 ♂♂ : 2100 h.; 2 ♂♂ : 2200 h.; A. fitchii: 1 ♀ : 2300 h. E1: A. flavescens: 1 ♀ : 2200 h. Evening: Very large numbers present in MacKinnon Ravine and at White Mud Creek, especially in clearing holes but not at edges of wooded area. MacKinnon Ravine: A. fitchii: 24 ♀♀; A. excrucians: 24 ♀♀; A. stimulans: 3 ♀♀; A. fitchii (?): 3 ♀♀. Horse pasture near White Mud Creek: A. fitchii: 12 ♀♀; A. excrucians: 1 ♀ ; A. flavescens: 3 ♀♀; A. trichurus: 2 ♀♀; A. punctor: 1 ♀. Rearing cages two miles east of city limit: A. fitchii: 4 ♀♀; A. increpitus (?): 1 ♀; A. implicatus: 1 ♀; A. flavescens: 1 ♀.

DATE	OBSERVATIONS
June 18	E5: A. stimulans: 1 ♂ : 0400 h; 3 ♀♀ : 2100 h.; A. flavescens: 1 ♀ : 2300 h. E1: A. fitchii: 1 ♂ : 0400 h.; 1 ♂ : 0800 h.; A. stimulans: 1 ♂ : 0400 h.; A. flavescens: 1 ♂ : 0800 h.
June 19	Little activity at meteorological sites and at sites of rearing cages. Rearing cages two miles east of city: A. flavescens: 4 ♀♀; A. fitchii (?): 1 ♀ ; A. communis: 1 ♂; C. alaskaensis: 1 ♂. E5: A. flavescens: 1 ♀ : 0100 h.-1000 h.; A. sticticus: 2 ♂♂ : 2300 h.; A. stimulans: 5 ♂♂ : 2200 h.; 17 ♂♂ : 2200 h.; 2 ♂♂ : 2400 h.
June 20	Late P. M. at White Mud Creek: very reluctant to bite: A. fitchii (?): 8 ♀♀; A. stimulans: 1 ♀; A. flavescens: 1 ♀; A. excrucians: 2 ♀♀. E1 not in operation.
June 21	E5: A. fitchii: 1 ♀ : 0200 h. E1: A. increpitus: 1 ♀: 1000 h.; C. alaskaensis: 1 ♀ : 1000 h.
June 22	Very little activity - no catches in the traps.
June 23	No attack at meteorological sites except in MacKinnon Ravine: A. excrucians: 5 ♀♀; A. stimulans: 2 ♀♀; A. fitchii: 14 ♀♀; A. increpitus: 1 ♀. E1 and E5: no catches.
June 24	E5: C. alaskaensis: 1♀: 0100 h.; 1 ♀ : 0200 h.; A. flavescens: 1 ♀ : 0300 h. E1: no catch.
June 25	E1: C. alaskaensis: 1 ♀ : 2300 h.; A. flavescens: 1 ♀ : 2400 h. E5: no catch.
June 26	E5: no catch. E1: C. alaskaensis: 2 ♀♀ : 0200 h.
June 27	E1 and E5: no catches.
June 28	E1 and E5: no catches. Golfers report a few mosquitoes present on Riverside Golf Course. Picnickers report presence of mosquitoes in Victoria Park.
June 29	E5: Culiseta sp.: 1 ♀ : 2100 h. E1: no catch.
June 30	No mosquitoes active at meteorological sites. E1 and E5: no catches.

Mosquitoes were present some places until the middle of July. Towards the end of June and thereafter mosquitoes were found in dense vegetation near the bottom of ravines. Elsewhere mosquitoes were found only in dense vegetation. Very few were caught in the traps after the third week in June.

A number of specimens of Culex restuans Theobald were taken. This constitutes a new record for this region.

2.7.1. Discussion of Observations of Adults with Special Reference to the Spatial Distribution of Adults.

The appearance of adults in the valley was not sudden. On May 17, 1958 huge swarms of Aedes cataphylla Dyar mosquitoes were observed on the Mayfair Golf Course. On every day in the week preceding May 17,except on May 13, adult mosquitoes were either trapped or observed. The full significance of these observations cannot be assessed since the manner in which the behavior of Aedes cataphylla mosquitoes varies with time is not known. The observations made suggest that Aedes cataphylla mosquitoes emerge, perhaps rest for a time, actively disperse, and then swarm and mate. On May 15 and May 16 biting mosquitoes were observed in moderate numbers; but no swarming was observed. After May 17, much swarming occurred on favourable evenings. Apparently, then, the mosquitoes observed on May 17, 1958 had just passed through the phase of dispersion. It follows that the mosquitoes observed were only a few days old.

It is reasonable to assume that number and size of swarms indicate adult density.

In the week following May 17 very many swarms were observed in the section of the river valley west of the University. In the residential

section along MacKinnon Ravine, there was, during this week, a very marked reversal in the attitude toward the mosquito trap which previously was thought to "mess up the boulevard." In the eastern part of the river valley, great difficulty was experienced in collecting a sample; few and only small diffuse swarms were seen. Golfers did not report mosquitoes.

Very few mosquitoes were seen in any part of the city other than in the river valley and adjoining ravines. Away from the valley and ravines only one small swarm was seen - and within a mile of the river valley. It should be pointed out that observations were not confined to the river valley.

During this week the species present in largest numbers was Aedes cataphylla.

On May 25, 1958, several specimens of A. fitchii and A. stimulans were taken. In the following two weeks mosquitoes with banded legs were taken every day except on May 29. By June 3, there was no longer any doubt that this complex of species was present in very large numbers. More difficulty was encountered in establishing the spatial distribution of this group of species than that of Aedes cataphylla because these species have different swarming habits. An estimate of the population density of A. fitchii was dependent on biting activity. Under unfavourable environmental conditions, it was necessary to disturb the mosquitoes resting in the vegetation in order to assess their density. In the northwest, north and northeast sectors of the study area, only few mosquitoes were present. However in the southern half of the city mosquitoes were present in all of the ravines and in the river valley. In fact the mosquitoes could not be found in significant numbers in any other

areas than the river valley and the ravines. Complaints were received from residents in the White Mud Creek, MacKinnon Ravine, MacKenzie Ravine and Wadhurst Road regions. The City Parks Dept. contemplated an adulticide program for these areas. The eastern part of the river valley was comparatively free from mosquitoes. Fewer mosquitoes appeared to be harboured on the Highlands Golf Course than on any other golf course. To be sure there were distinctly more mosquitoes in the western portion of the river valley than in the eastern portion.

2.7.1.1. The possible influence of surface winds on the dispersion pattern.

The most obvious ways by which mosquitoes could arrive from a source region to another region are:

1) wind directed flight.

2) passive transport by surface winds.

3) transport by storm cells.

By an examination of the wind data it was established that the wind directions were exceedingly variable during the periods when mosquitoes were apparently infiltrating the control area. To be sure, from the raw wind data one could not establish the direction from which the mosquitoes had come. However it was known that mosquitoes could not possibly have been active during all hours because of limiting environmental conditions. The meteorological data was grouped into Table 4 on an hourly basis, and estimates of possible activity were made. In order to estimate the activity of the mosquitoes, it was assumed that activity would be non-existent or light in temperature $< 50^{\circ}$F.; R. H. $< 30\%$; wind > 12 m.p.h. In Table 4 opposite "activity", L means little or no flight, M means

moderate amount of flight, H means flight activity is high.In Table 4, the row designated as "activity" is the activity predicted from a consideration of meteorological data.

The number of hours during which the mosquitoes could have been active were grouped according to the mean direction of the wind during each hour and the corresponding wind mileage was calculated (Tables 5 and 6). Each sum is represented by the length of the vector in the vector diagrams. (Fig.5)

In order to determine the possible wind influence, the periods of May 10-May 17 in the case of Aedes cataphylla and May 25-June 3 in the case of Aedes fitchii, A. stimulans and A. excrucians were treated in the above described manner.

According to the hourly wind direction records, both refined and unrefined, one should have expected to have found the mosquitoes distributed all over the city. Moreover since most of the larval habitats were to the northwest of the city, one should have at least expected a high population in the northwestern part of the city. The wind direction records cannot indicate whether the mosquitoes came from a given locality; nor do they explain the pattern of distribution observed within the city.

2.7.1.2. Influence of the passage of cold fronts.

A very active cold front passed over the city at 0400 hrs. on May 12. There was however no obvious increase in the mosquito populations accompanying this event. According to the data obtained from the rearing cages, very few mosquitoes emerged prior to May 13. In the remaining period from May 13 to May 17, no cold fronts passed over the region. There is no possibility, therefore, that population of Aedes cataphylla

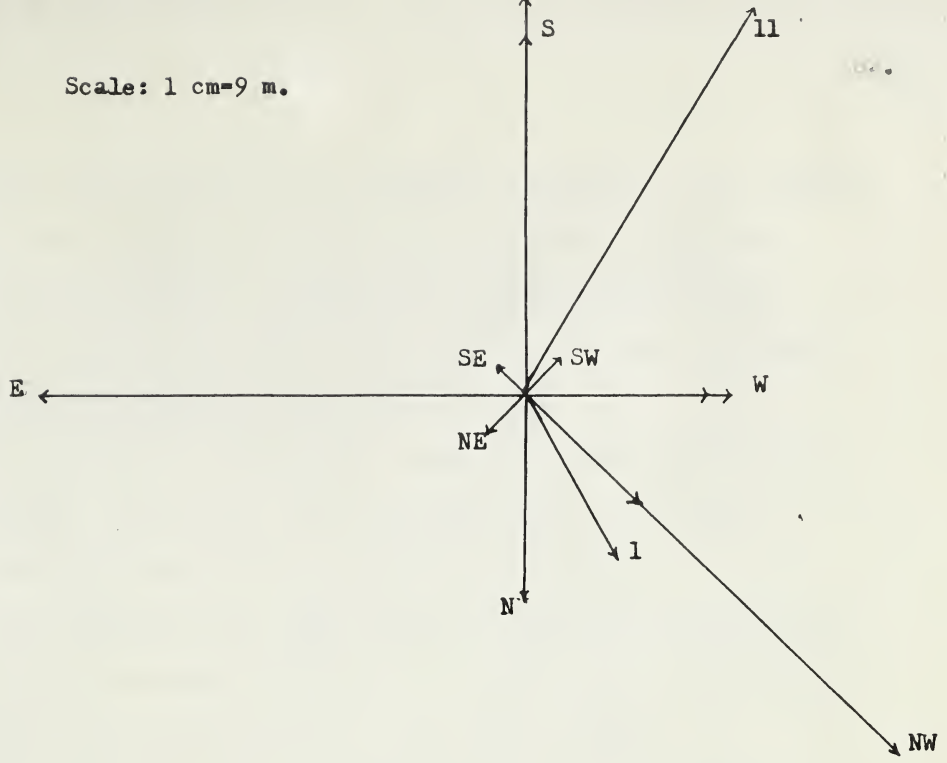
Table 5. Number of hours when environmental conditions would not suppress mosquito activity and the corresponding wind mileages.

Date	Wind Direction S	SW	W	NW	N	NE	E	SE
May 14	2-21							
May 15	3-29		2-18					
May 16			1-7	2-19				
Subtotal	5-50		3-25	2-19				
May 10	1-4		1-6	6-41	2-18	1-6	5-37	1-5
May 11							4-22	
May 12				1-11	1-7			
May 13	1-2	1-6						
Grand total	7-56	1-6	4-31	9-71	4-25	1-6	9-59	1-5

Little emergence

Table 6. Number of hours when environmental conditions would not suppress mosquito activity and the corresponding wind mileages.

Date	Wind Direction S	SW	W	NW	N	NE	E	SE	
May 28		4-14	3-13		1-7		4-27	1-9	
May 29	1-5				1-5	6-54	3-25	3-13	
May 30					4-22	3-23	1-5		
May 31	4-34							2-20	
June 1	3-21					2-22	5-45	2-12	
June 2	2-9	2-11	3-15	2-8		1-4	4-17	1-3	
June 3			1-5	1-5	2-15	5-28			
Subtotal	10-60	6-25	7-33	3-13	8-49	17-131	17-119	9-57	
May 25	1-9	2-18		1-11	3-28				Little emergence
May 26		2-6	3-9	2-14	1-9	1-3			
May 27	3-10	6-45	2-4						
Grand total	14-79	16-94	12-46	6-38	12-86	18-134	17-119	9-57	



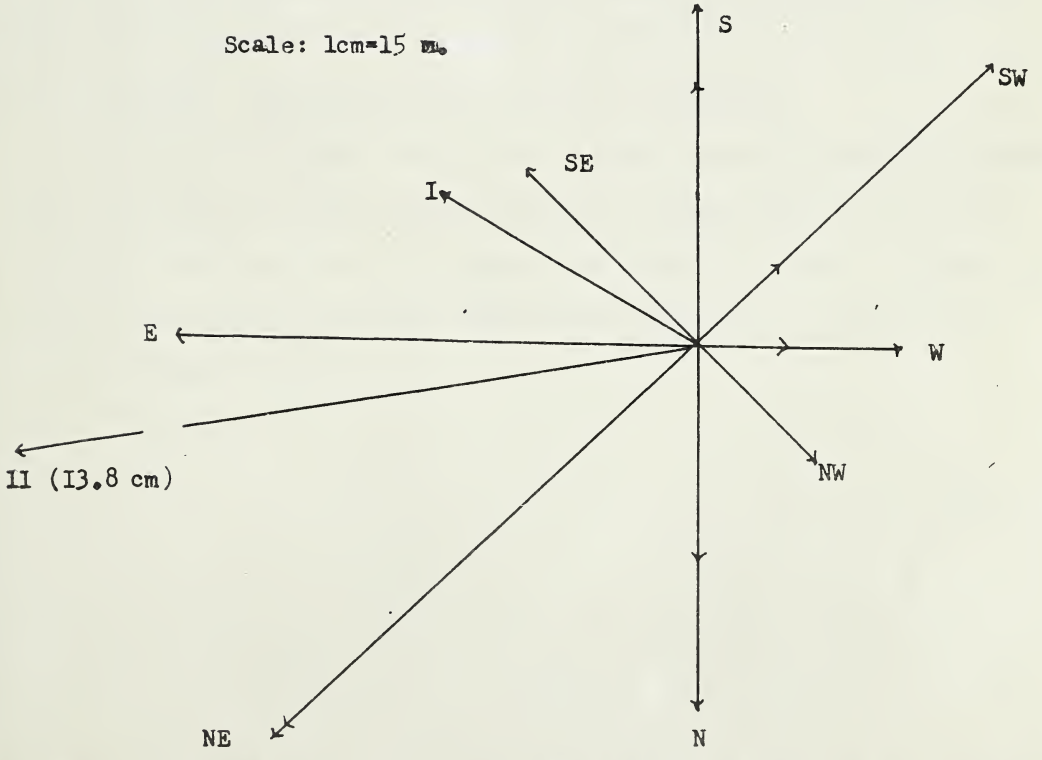


Fig. 5. Wind mileage during hours when mosquitoes could exhibit spontaneous activity. In the upper figure, vector I is the resultant for May 10, 1958 to May 16, 1958. Vector II is the resultant for May 14, 1958 to May 16, 1958. In the lower figure vector I is the resultant for May 25, 1958 to June 3, 1958. Vector II is the resultant for May 28,1958 to June 3, 1958.

was transported into the city in this instance. Moreover, if such transport had occurred, the population should have had a city-wide distribution.

In the period from May 25 to June 3, when Aedes fitchii species complex appeared in the city, only one cold front passed over the region. This front passed the airport at 0353 hrs. on May 25.

The first specimens of this species complex were taken the day that the front passed. It is hardly surprising that only a few of these mosquitoes were taken since few had emerged before May 27.

There is no doubt that the large numbers of mosquitoes which appeared in the river valley appeared independently of the passages of cold fronts.

2.7.1.3. The possible influence of the city's lights.

According to Horsfall (1955) city lights may attract mosquitoes. One should have expected a city-wide distribution if the glow of the city lights were responsible for the presence of mosquitoes in the city.

2.7.1.4. The influence of the moon on dispersion.

The hours during which the moon was visible and during which mosquitoes could have been active are given in Table 7. However there is no way of evaluating the importance of the moon in the observed pattern of dispersion since no data was obtained that would allow a comparison of activity on dark and moonlit nights.

Table 7. Hours when moon may have influenced dispersion.

Date	Hrs.	Wind	Predicted Activity	
May 10	0200	N11	M	May 10 - May 17
	0300	N14	M	
May 11	0100	E12	M	
	0200	E12	M	
May 12	0100	N7	M	
	0200	NW11	M	
Total hours	6			
May 25	2200	N10	M	May 25 - June 3
	2300	N8	M	
	2400	N10	M	
May 27	2200	SW9	M	
	2300	SW8	M	
	2400	SW11	M	
June 2	2100	SW5	M	
	2200	SW6	M	
	2300	S7	M	
	2400	W5	M	
Total hours	10			

3. CONCLUSIONS

3.1. THE ORIGIN OF MOSQUITOES IN THE RIVER VALLEY.

Since most of the larval habitats were located to the northwest of the city, one might postulate that the mosquitoes either flew in or were blown in from the northwest. If this were the case, mosquitoes should have been found in largest numbers in the northwestern sector of the city. However, despite the fact that suitable resting places were available, few mosquitoes were to be found in the northwestern part of the city. Moreover, if the mosquitoes had blown or flown over from the northwest, the distribution of adults in the river valley should have been more or less uniform. The same would be true if the mosquitoes had been blown in or had flown in from any other direction.

There are reasons to believe that the movements of mosquitoes over the plain must have been very limited. Long range movements of mosquitoes are likely to occur if the mosquito will fly several feet above the ground. So long as a mosquito can resolve the background, upwind flight will occur providing the mosquito is near the ground and windspeeds are lower than the mosquito's preferred maximum airspeed. Upwind flight will not result in a very great displacement. To illustrate, assume a mosquito has energy reserves to fly 30 miles. Further assume a uniform headwind of 3 miles per hour and that the mosquito is flying at 3.5 miles per hour. The maximum distance that the insect is able to fly is $\frac{0.5}{3.5} \times 30 = 4.3$ miles. Certainly one would expect the actual displacement to be less than 4.3 miles. Smith (in litt. 1959) has evidence that mosquitoes disperse from a pool at a rate of about one mile in twenty-four hours.

To fly against the wind from the edge of the control area to the city center, a mosquito would have to "refuel." The flowering plants necessary for "refueling" are unlikely to be found in great abundance on the intervening cultivated farm land.

The question may be raised: what will prevent a mosquito from gaining altitude and hence from taking advantage of the wind? Sutton (1953) has summarized information regarding the water-vapour profile. It has been found that the water-vapour profile has the same shape as the wind profile. Rider (1954) published some very accurate measurements on the profiles of wind, temperature and water-vapour and his results are in good agreement with Sutton's concept. During large inversions however the relationship between the wind profile and water-vapour profile is destroyed. Under conditions of large inversions, the vapour pressure may increase with height. As the writer understands, this situation is depicted in the results published by Pasquill (as cited by Sutton, 1953, p. 317.) The data summarized by Geiger (1950) also support this notion.

It may be readily seen, then, that if the relative humidity is say 30% or 40% as it was during the month of May, dispersing mosquitoes will find the air most favourable near the earth's surface. That mosquitoes are sensitive to vertical humidity gradients has been borne out by the work of Pittendrigh already cited. Moreover if mosquitoes find a suitable resting place, they cannot be expected to venture forth into far less favourable conditions of humidity.

There is one possible route that mosquitoes may have taken into the city without exposing themselves to unfavourable environmental conditions.

This route is along the river valley. Meteorological data has already been presented which indicated that during hours of darkness and during cloudy periods, windspeeds were generally lower within the valley than on the plain. Further, the saturation deficiencies were lower in the valley than on the plain. It was obviously possible for mosquitoes to be active within the valley for many hours when the severity of meteorological conditions on the plain ruled out activity. Activities such as swarming which are controlled by light intensity can be carried on as late in the evening within the valley as on the plain (Nielsen and Nielsen, 1958). Migration along the river valley would result in a more gradual decline in numbers with distance from the source than if dispersion from the source took place in all directions. Certainly along several miles of the river valley southwest of the Mayfair Golf Course, the mosquito population density was quite high.

3.1.1. The Valley as a Rectifier.

How does the valley "canalize" the movements of mosquitoes? The responses of mosquitoes to environmental variables during the period when they disperse have not been studied. Nielsen and Nielsen (1953) found that certain "migratory mosquitoes", Aedes taeniorhynchus, exhibit a marked tendency to disperse shortly after emergence. After this initial tendency to disperse, the whole behavior pattern of these mosquitoes changes.

However, in the case of Northern Aedes we do not know whether the tendency to disperse is confined to a sharply delimited period of the adult's life. In attempting to explain the rectifying action of the river valley, then, must we understand the responses of mosquitoes during a

sharply delimited period or throughout the adult's entire life span?

Nothing is known of mosquito behavior in turbulent air; but might not eddies formed at a valley's rims constitute a barrier to dispersion? Eddy formation is dependent on the prevailing lapse rate, curvature of the bank and wind velocity. Morgan (1931) indicated that eddies at the rim of a valley are not formed in windspeeds less than 10 m/sec. Since winds are very light during twilight hours when mosquitoes are active, eddies cannot be the only rectifiers. Swarms of Aedes cataphylla were often observed just above the valley rim.

Perhaps differences in relative humidity on the plain end in the valley might be operative in orthokinetic or klinokinetic behavioral mechanisms which could confine mosquitoes to the valley. However, all behavior exhibited by mosquitoes cannot be explained simply in terms of taxes and kineses. Nielsen and Nielsen (1953) established that males of Aedes taeniorhynchus repeatedly swarm at a given site. Since past experience can influence mosquito behavior, it seems reasonable to postulate that mosquitoes would be prone to remain in the valley if the environment were less favorable on the plain.

The high population densities in the ravines are probably related to the nocturnal air drainage down the ravines. It is suggested that mosquitoes in the valley respond in an anenomo-positive fashion to this air drainage which must extend into the valley. Of course, skototaxis may also be involved in this process since the mouths of the ravines appear as dark areas at night.

The mechanisms which caused the continued presence of the mosquitoes in the ravines are doubtless identical to those which canalized their

flight down the valley.

3. 2. DISCUSSION.

In the literature on mosquitoes one frequently finds a statement to the effect that topography influences the pattern of dispersion (see Horsfall, 1955). Very little evidence is presented to support this hypothesis. De Meillon (1933) as cited by Horsfall (1955) found that dispersion of mosquitoes was restricted to wooded river valleys of Transvaal during dry seasons. According to the map of adult distribution in the work of Stage et al. (1937) Aedes vexans and Aedes aldrichi disperse along tributaries. Causey et al. (1948) collected most of the tagged mosquitoes along the river valley; however, recoveries were low. Shemanchuk et al. (1955) collected those tagged mosquitoes which flew furthest from the point of release within the river valley. Unfortunately the hypothesis that the topography may exert an influence on dispersion is not readily evaluated from tagging experiments. Certainly part of the topographical influence must be that due to local winds.

MacLeod and Donnelly (1958) released blow-flies in hilly country. These workers concluded that the flight of individual flies is random. Moreover they state that "Oriented reactions, however, or even klino-kineses, to microgradients of temperature pressure air movement or reflectance from the ground below them, might reasonably have been expected to influence the direction of the dispersal paths of the individuals of each species, in relation to ground masses and plains, or their cover so that they would tend to be shepherded towards the arenas favourable for the species. There is no evidence of such orientation of flight."

Even if these authors had obtained much higher recoveries of marked specimens and if the traps sampled a volume of air of constant dimensions one wonders whether they had the necessary micrometeorological data necessary to draw such conclusions. In hilly country windspeeds and directions constitute a very complicated pattern. This pattern,as well as the other environmental variables,undergoes very great changes throughout the day. To be sure katabatic winds and the characteristics of air within the first few meters of the earth's surface are very poorly understood. That one cannot extrapolate readings from one meteorological station over an irregular topographic region is stressed in the writings of micrometeorologists. It seems reasonable to expect that if the environment were really understood, and if the reactions of the insect to the environmental variables were understood, then one should be able to predict the displacement of the insect. One cannot repeatedly demonstrate various responses of an insect under controlled conditions and then assume that these responses are not operative in the natural environment.

Kennedy (1951) has reviewed evidence that the movements of the migratory locust may be canalized along valleys. This author has suggested that such movement is "consistent with the principle of movement in the direction of maximum constancy of the visual field." One need not, however, expect canalization in all cases. The migratory locust is indeed a special case since it has much better control over its track, and because of its excessive "locomotory drive." An organism, such as a mosquito which flies at a very low speed will be much more subject to localized changes in the wind. Moreover, an insect which is prone to exhibit telotactic responses to minor irregularities in its visual field

or respond to non-visual stimuli such as odour, temperature and humidity gradients may not show "canalized" movements.

During the course of this investigation, Hocking suggested that insects above large bodies of water steadily fly with wind because the moving waves prevent the insect from getting the impression that it is being displaced. Similarly insects above the river might be led into the city by the moving pattern on the water surface. To test this suggestion, observations on the evening of May 26 were made from a row-boat. A very gentle breeze blew from the east. Moths were seen to fly in all directions over the water. Mosquitoes on the other hand were observed only following the boat. The water was exceedingly muddy but the reflection of the banks could be seen as the dominant pattern upon which the wavelets were superimposed. Had the waves been large, the visual situation might well have been reversed. However, under such conditions, mosquitoes would not have any control over their track.

The source of the mosquitoes has not been established. There are two possibilities: either the mosquitoes originated in pools within the river valley, or they originated in pools on the plain above the valley.

The second possibility demands a mechanism whereby the valley accumulates mosquitoes. The behavior of wind passing across a small valley has not been investigated. However, cross winds have been studied in the Columbia River Valley for the period April 11 to August 31, 1939 (Hewson and Gill, 1944). The valley is about 16,400 ft. wide by about 3,300 ft. deep. In the period from 0100 hr. to 0300 hr. no eddies are formed; the wind penetrates to the valley floor but the velocity decreases rapidly with increasing depth. At 0500 hr. complete air circulation of the

air in the valley begins near the valley floor. During the forenoon this circulation becomes quite well developed over the whole cross-section of the valley. By 1300 hr. this circulation has completely disappeared and the wind again penetrates to the floor of the valley but with a greater force than at 0100 hr. By 2100 hr. the overhead wind has subsided and a circulation begins in the valley. This circulation has completely subsided by 0100 hr. and the wind again penetrates to the valley floor.

An insect carried by the wind in the 0100-0300 hr. period would rapidly lose altitude as it passed over the rim of the valley. If the insect were in an airstream penetrating to the valley floor, where the windspeed becomes greatly reduced, the insect could then govern its own track.

During the 0500 hr. till noon period the wind-borne insect might readily be deposited in the valley by circulation. This would also be the case in the 2100 hr. to midnight period.

During the afternoon when the wind penetrates to the valley floor with undiminished force, deposition of an insect would depend on the insect's behavior rather than on the wind characteristics.

Morgans(1931) reviewed the literature on the relation of ground contours and the characteristics of wind. According to this review unstable eddies may form in the lee of an obstacle in winds less than 10 m./sec. (ca. 22 m.p.h.) Such an eddy could effectively deposit wind-borne insects.

The displacement of an insect approaching the valley rim from an upwind direction is problematical. Only if the insect were flying so low

that its air speed were greater than the windspeed would entry into the valley be easily effected. The entry into the valley of an insect flying several meters above the ground would be hindered by the wind because the vertical component of the wind increases markedly at the downwind rim of the valley.

Meteorological events in the valley of the North Sask. River have been described,and the agreement between these observations and those made in the Columbia River valley is encouraging.

It seems, therefore, that the probability of a wind borne mosquito being deposited in the North Sask. River valley is high especially during the normal activity period of mosquitoes.

3.3. RECOMMENDATIONS.

It is recommended that a "barrier strip" of 3% Lindane be laid down across the valley outside of the city limits. Moreover the efficacy of this measure should be evaluated. If this measure is highly successful, the efficacy of a D D T barrier strip should be evaluated in the hope of long term protection.

3.4. SUGGESTIONS FOR FURTHER RESEARCH.

To be able to predict where an insect or group of insects will be found after a given time interval has elapsed since the position of the insect or of the group of insects was last established, one must understand both insect and environment.

The laboratory studies on the responses of mosquitoes have proven most helpful but are inadequate in that they provide no information (except in extreme instances) about what the animal is doing in the field. That the behavior of mosquitoes varies with time is vaguely comprehended. The only detailed accounts in the literature relating to the changes in

behavior that occur with time are those dealing with Aedes taeniorhynchus. To make a practical illustration of our ignorance of mosquito ethology, one need only point out that it is not known whether northern Aedes mosquitoes disperse only during a well defined period of their adult life. However, even if one had a foreknowledge of what kind of activity a mosquito would exhibit, one could not in some instances predict the displacement of the mosquito under known environmental conditions. This is so because a quantitative understanding of sensory physiology - especially of the compound eye - is lacking.

The science of micrometeorology is still in its infancy. The meteorology of valleys has been investigated only in a few large valleys. What environmental conditions will confront an organism at any point of its environment at a given time cannot be predicted in most instances and certainly not in hilly country.

To obtain a deeper understanding of dispersion, then, the behavior of the insect and its environment must be quantitatively characterized.

The investigator in carrying out field studies is confronted with the formidable task of drawing samples representative of the numbers of mosquitoes above a given area. Sampling methods and experimental designs must be devised which allow for the fact that what an animal does may change with time. The lack of correlation between the numbers of adults trapped and the number of larvae from which the adults emerged as observed by Shemanchuk (1958), strikingly demonstrates the fact that sampling procedures do not allow for changes in behavior.

The height-density profile needs further characterization in non-wooded regions. The rate of vertical exchange within such a profile must

be determined in order that the efficacy of variously situated barrier strips can be evaluated.

The preferred angular velocity and preferred air speed of various species should be measured in the laboratory. Optomotor theory is basic to an understanding of dispersion. Such measurements should be made over a meaningful range of temperatures, humidities and stabilities of the air.

The optomotor theory as presented in this thesis requires extension to all heights and to all dimensions. The number of insects varies with altitude according to the relationship $f(R) = C\ (R + Ro)^{-\lambda}$. The proportion of a population of insects that will orient to a given angular velocity is given by the relationship $f(\omega_R) = k\ (e^{-\frac{\Delta\Phi}{\omega_R \tau_E}} - e^{-\frac{\Delta\Phi}{\omega_R \tau_D}})$. Hence at a given height R, the actual number of insects which will orient, is equal to $C(R + Ro)^{-\lambda}\ k\ (e^{-\frac{\Delta\Phi}{\omega_R \tau_E}} - e^{-\frac{\Delta\Phi}{\omega_R \tau_D}})$. If wind did not vary with height this expression could be used to calculate the total number of insects in the atmosphere which would orient, by making use of the relationship $v = \omega_R R$. However, windspeed increases with height according to the relationship $v = a R^{\frac{1}{7}}$. By making use of the appropriate substitutions and integrating the total number of responsive insects would be known. One further modification is necessary. The integral should be divided in two in order to calculate the number of insects flying upwind and the number flying downwind. To achieve this last end the integration must be done for wind velocities (or the equivalent values of R or) - ranging from V_{MT} to the insect's maximum air speed. This integral would give the number flying upwind. The symbols λ , C, a , Ro are constants.

Experimental studies on dispersion involving the use of marked specimens have been of limited value in the past. Much can be learned about what a species does simply by observing it in the field and by

studying it in the laboratory. Certainly the release of tagged specimens yields little information other than of local value unless the habitat is well understood, i.e. especially the characteristics of the layer of air near the ground above the site of the experiment.

The vertical distribution of mosquitoes in a vertical humidity gradient should be studied in the laboratory. Moreover the daily march of the humidity profile should be determined over surfaces of land with various coverings of vegetation, and of various soil types under a range of moisture conditions.

The variation of the locomotory drive with age of mosquitoes should be investigated. If the tendency to disperse is restricted to a well defined period, observed patterns of dispersion could be better evaluated in terms of environmental variables.

Since significant advances have been made in the theory of diffusion of gases within the lower layers of the atmosphere, the stimulation threshold of human odour in mosquitoes should be determined so that the attractiveness of a city due to human odour could be calculated.

The influence of the city lights on movements of mosquitoes should be evaluated.

Quantitative data regarding the densities of mosquito populations in various sections of the river valley should be obtained.

An aerological investigation should be carried out in the river valley. The nocturnal drainage of air down the ravines should also be investigated.

Since the movement of mosquitoes is dependent on a nectar supply, the sources of nectar should be established and mapped. Intensive control of

mosquitoes in regions adjoining the nectar supply might be advantageous.

It would be of interest to investigate the extent of dispersion on the plain.

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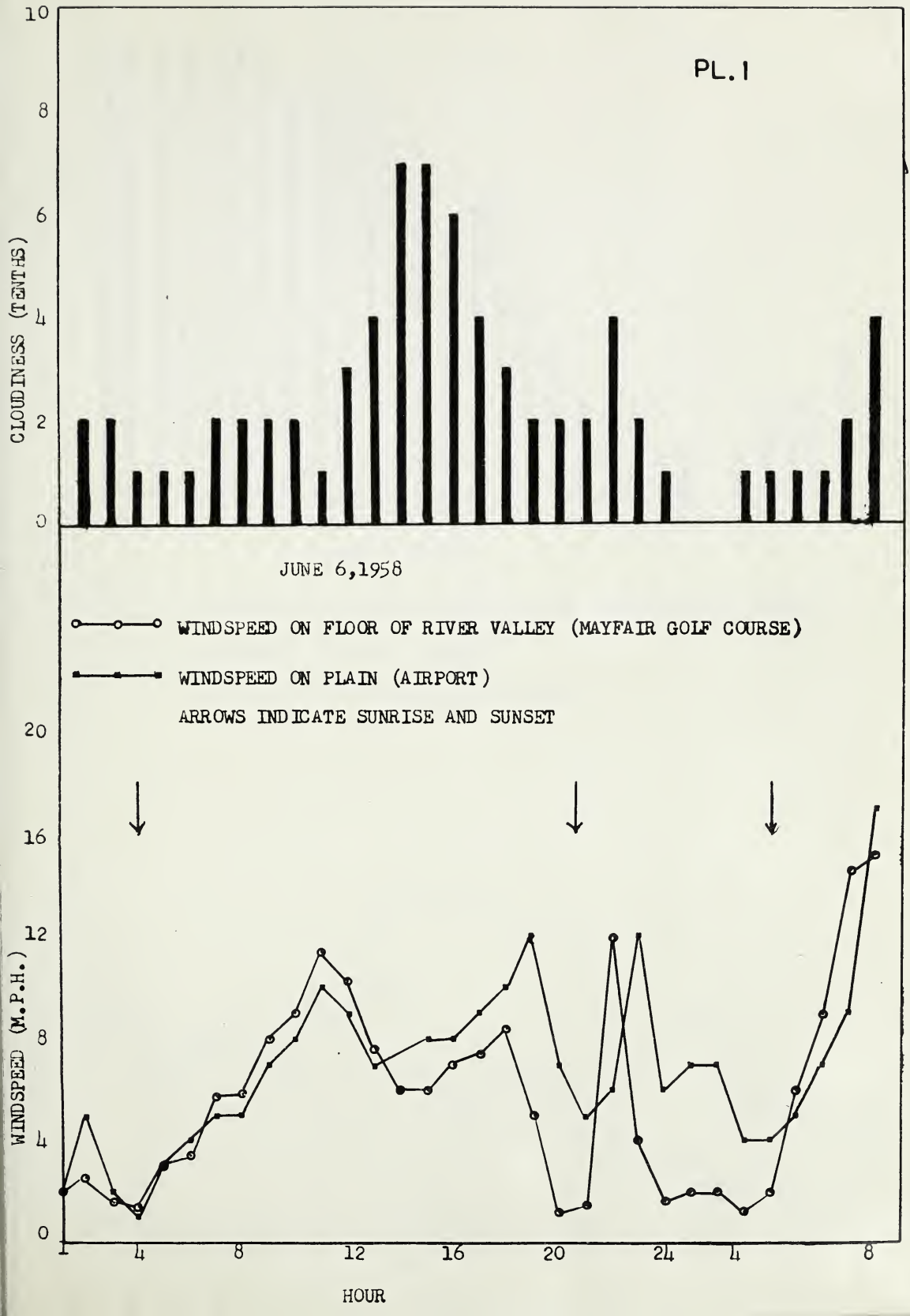
5. APPENDICES.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8
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4
2
0
JUNE 6,1958
WINDSPEED ON FLOOR OF RIVER VALLEY (MAYFAIR GOLF COURSE)
WINDSPEED ON PLAIN (AIRPORT)
ARROWS INDICATE SUNRISE AND SUNSET
WINDSPEED (M.P.H.)
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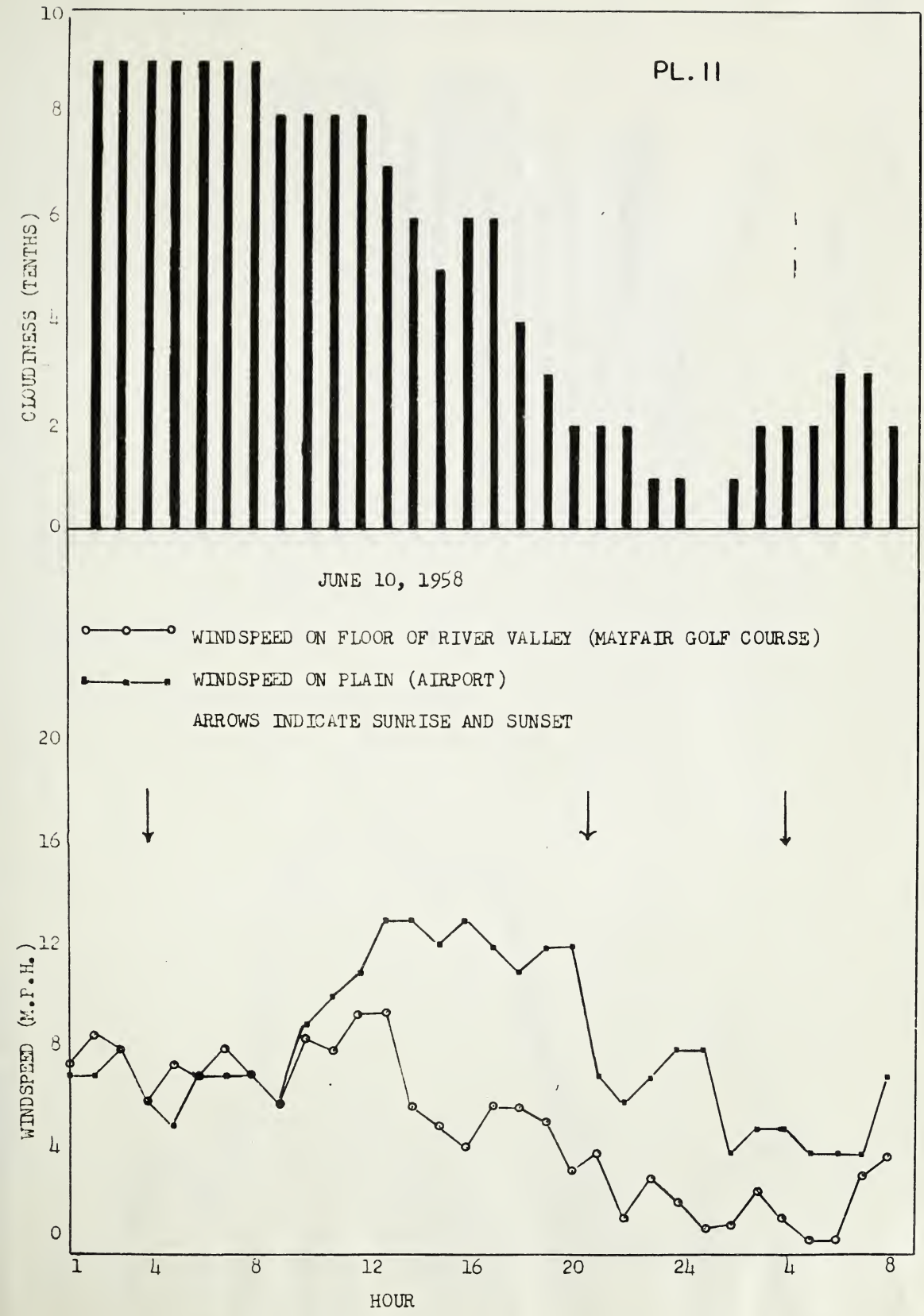
HOUR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JUNE 10, 1958
WINDSPEED ON FLOOR OF RIVER VALLEY (MAYFAIR GOLF COURSE)
WINDSPEED ON PLAIN (AIRPORT)
ARROWS INDICATE SUNRISE AND SUNSET
WINDSPEED (M.P.H.)
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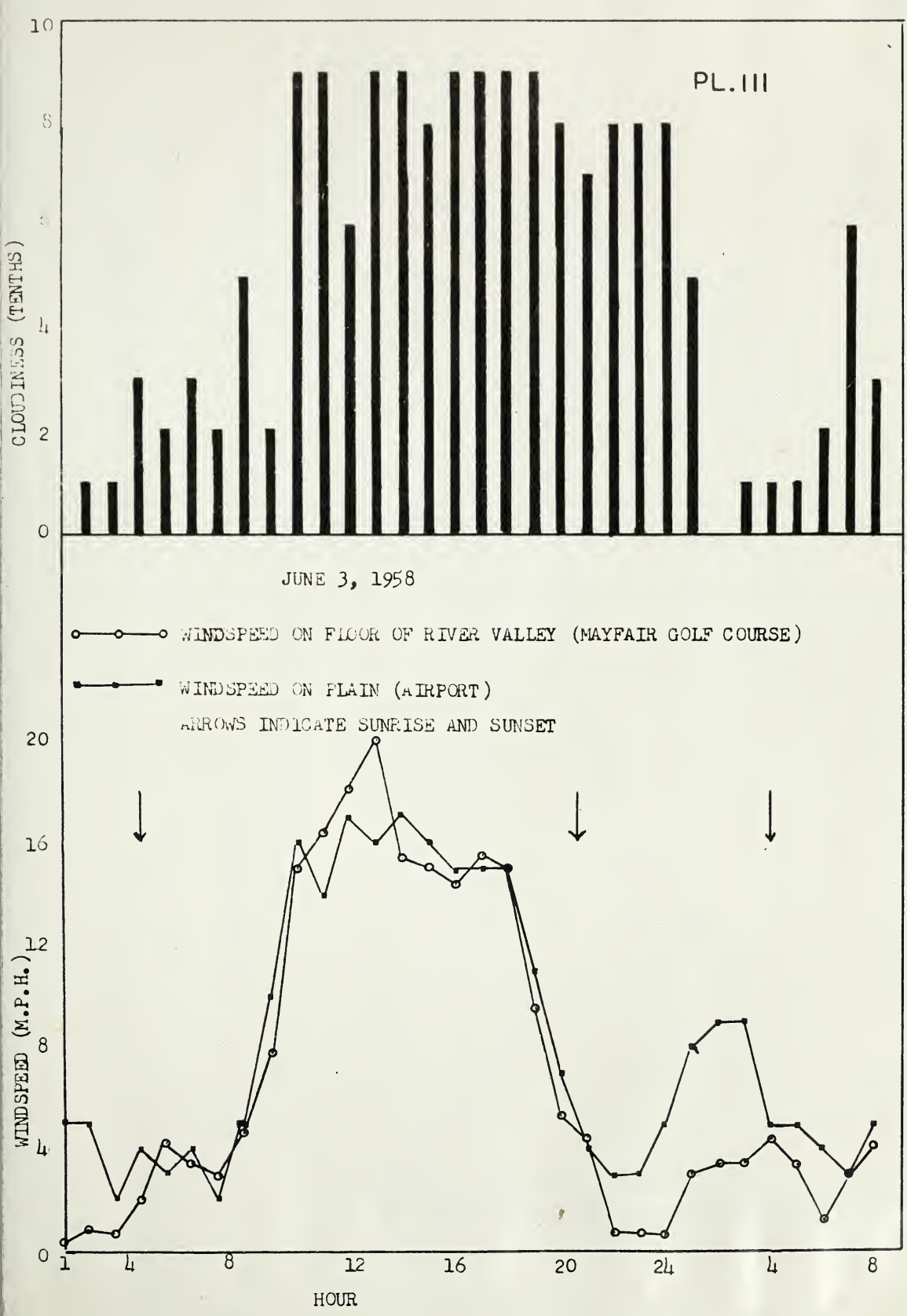
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JUNE 3, 1958
WINDSPEED ON FLOOR OF RIVER VALLEY (MAYFAIR GOLF COURSE)
WINDSPEED ON PLAIN (AIRPORT)
ARROWS INDICATE SUNRISE AND SUNSET
WINDSPEED (M.P.H.)
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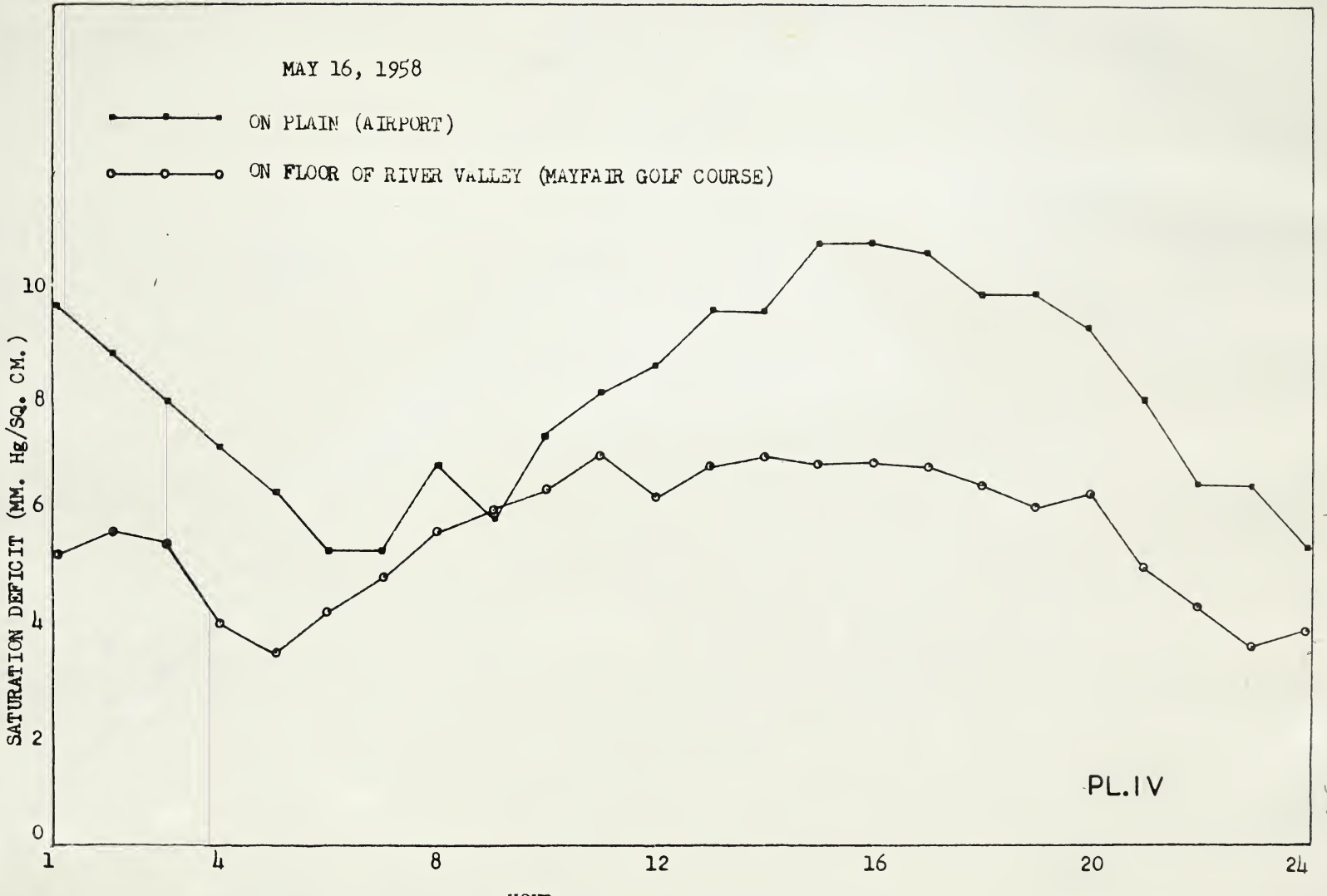
MAY 16, 1958
ON PLAIN (AIRPORT)
ON FLOOR OF RIVER VALLEY (MAYFAIR GOLF COURSE)
SATURATION DEFICIT (MM. Hg/SQ. CM.)
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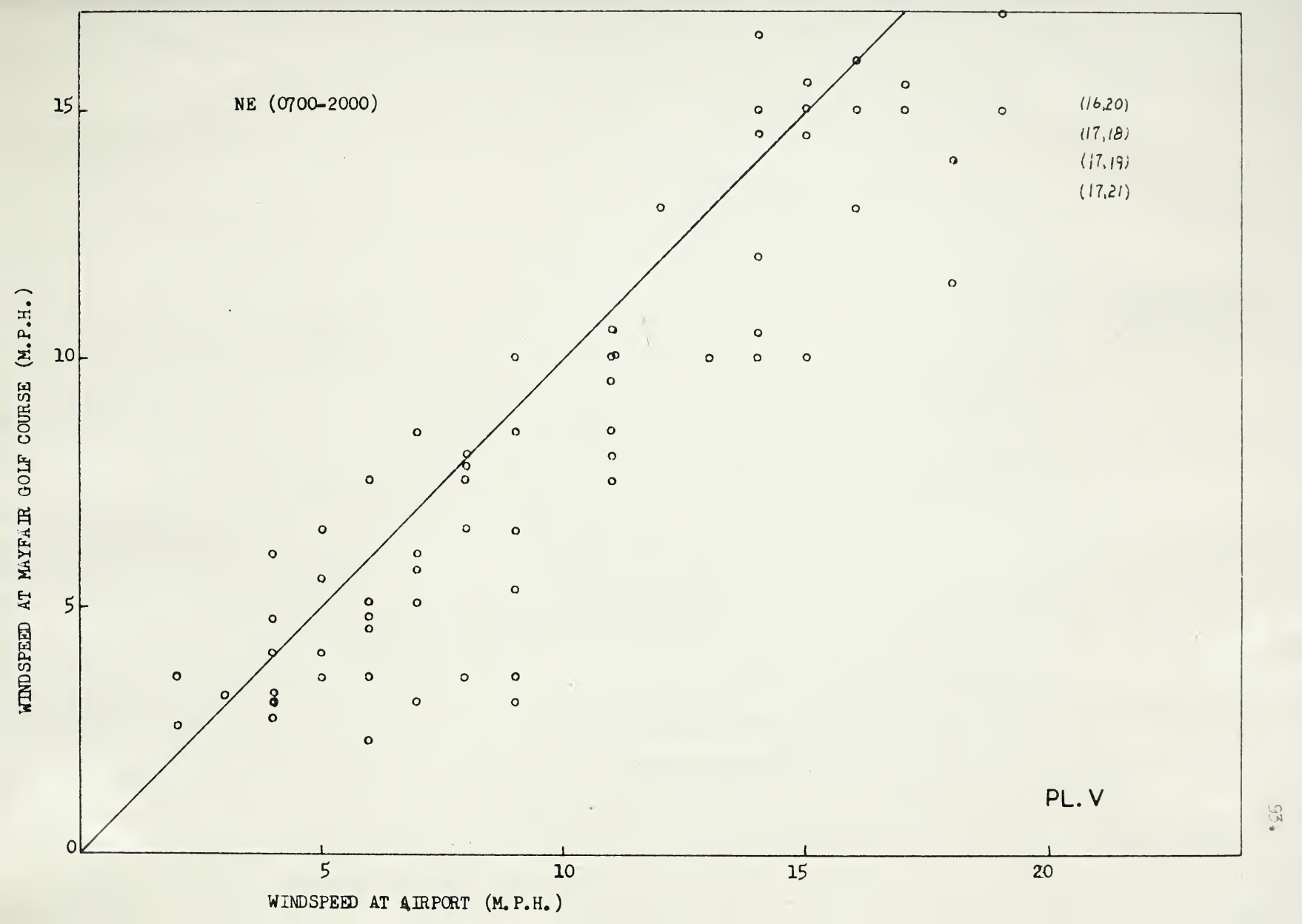
PL.IV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WINDSPEED AT MAYFAIR GOLF COURSE (M.P.H.)
WINDSPEED AT AIRPORT (M.P.H.)
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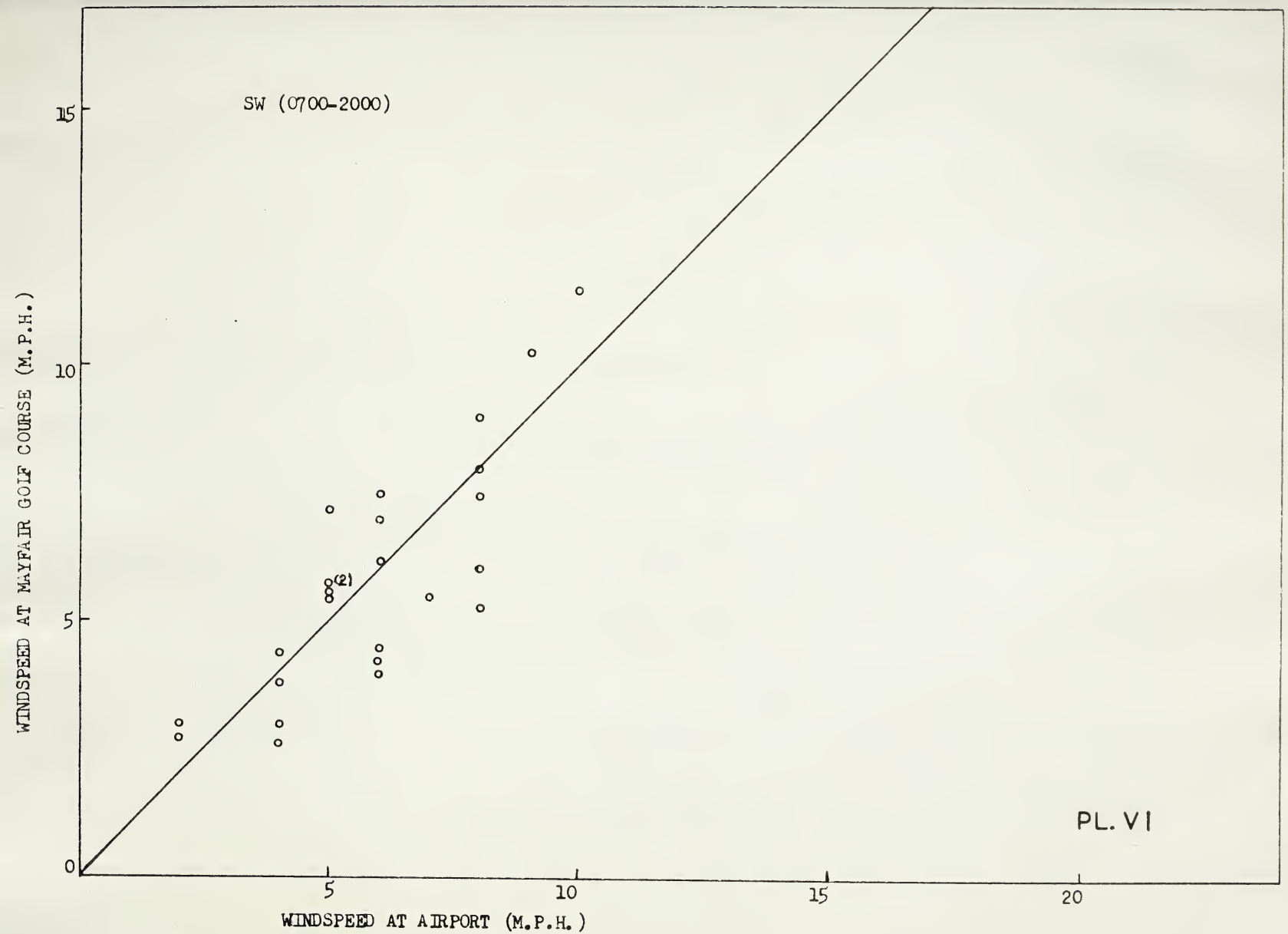
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WINDSPEED AT AIRPORT (M.P.H.)
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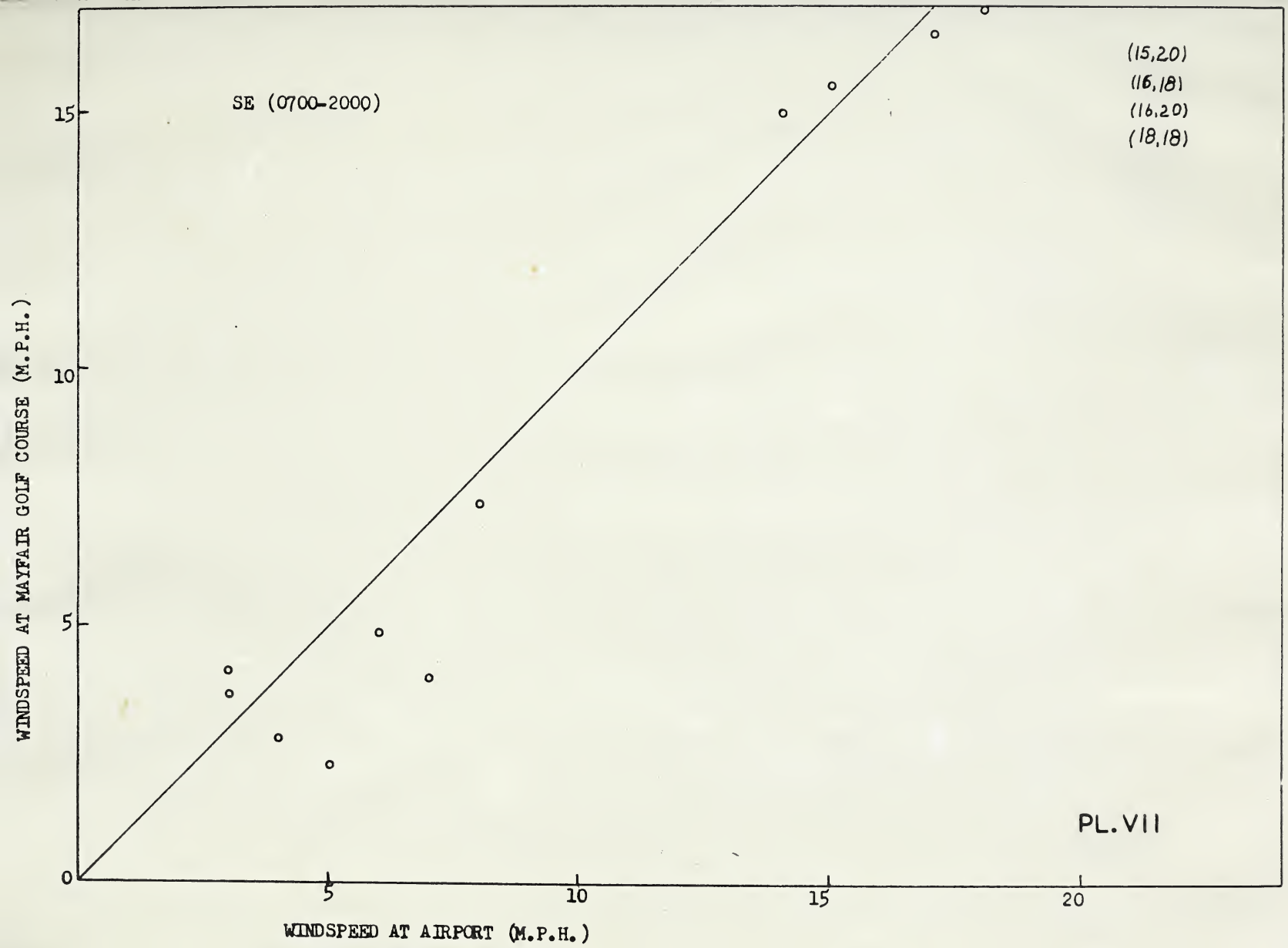
PL. VI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WINDSPEED AT AIRPORT (M.P.H.)
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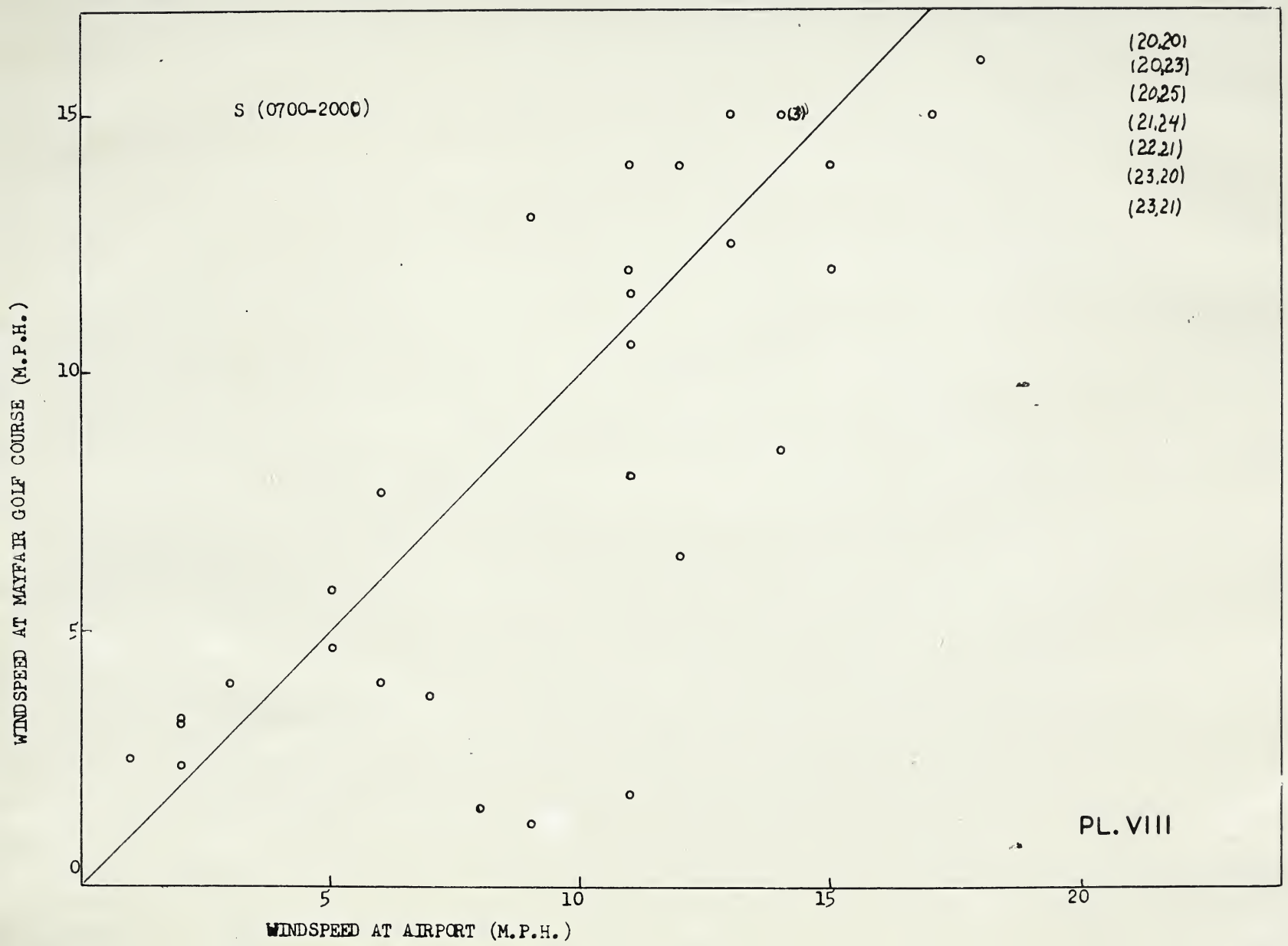
PL. VII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WINDSPEED AT MAYFAIR GOLF COURSE (M.P.H.)
WINDSPEED AT AIRPORT (M.P.H.)
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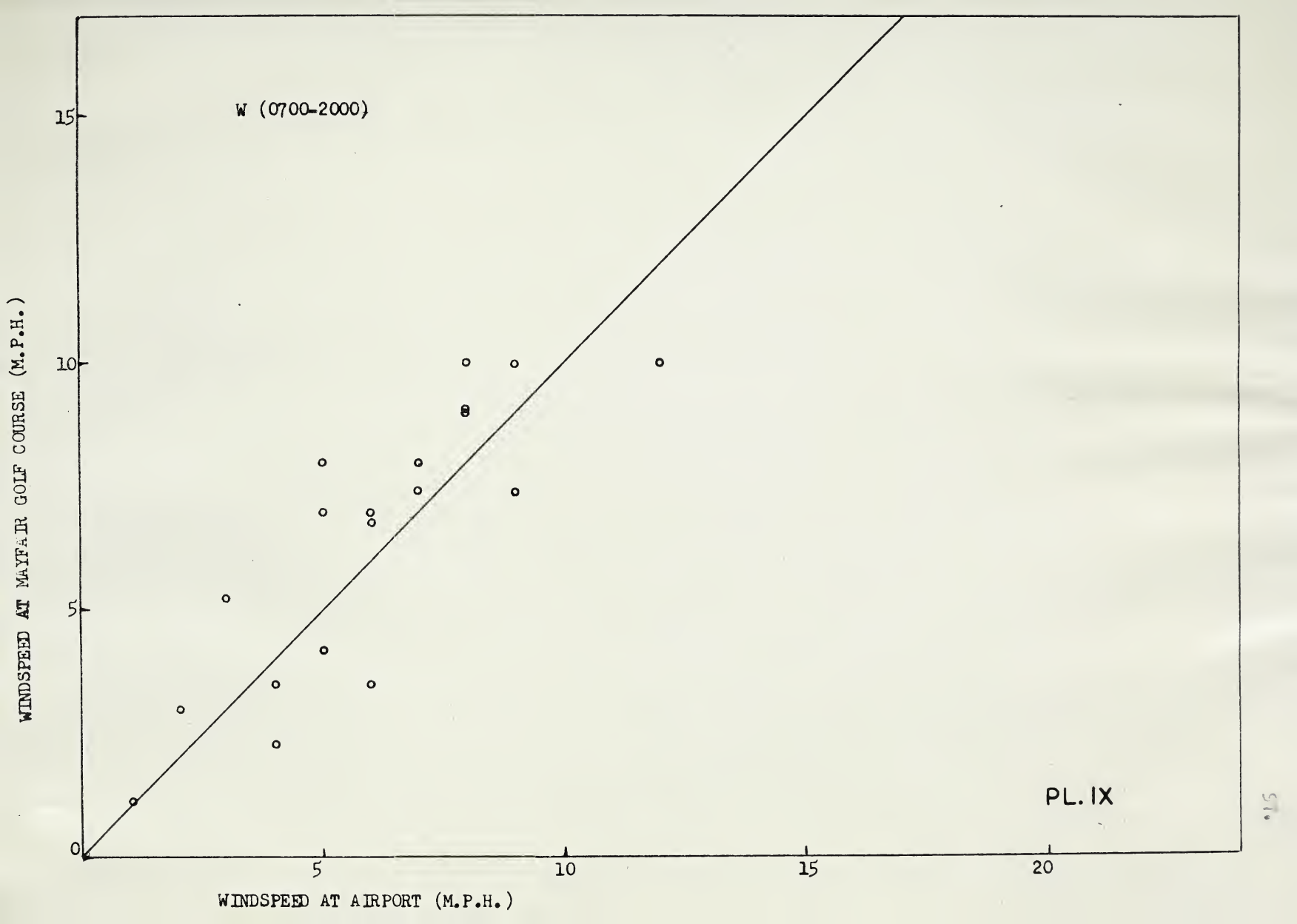
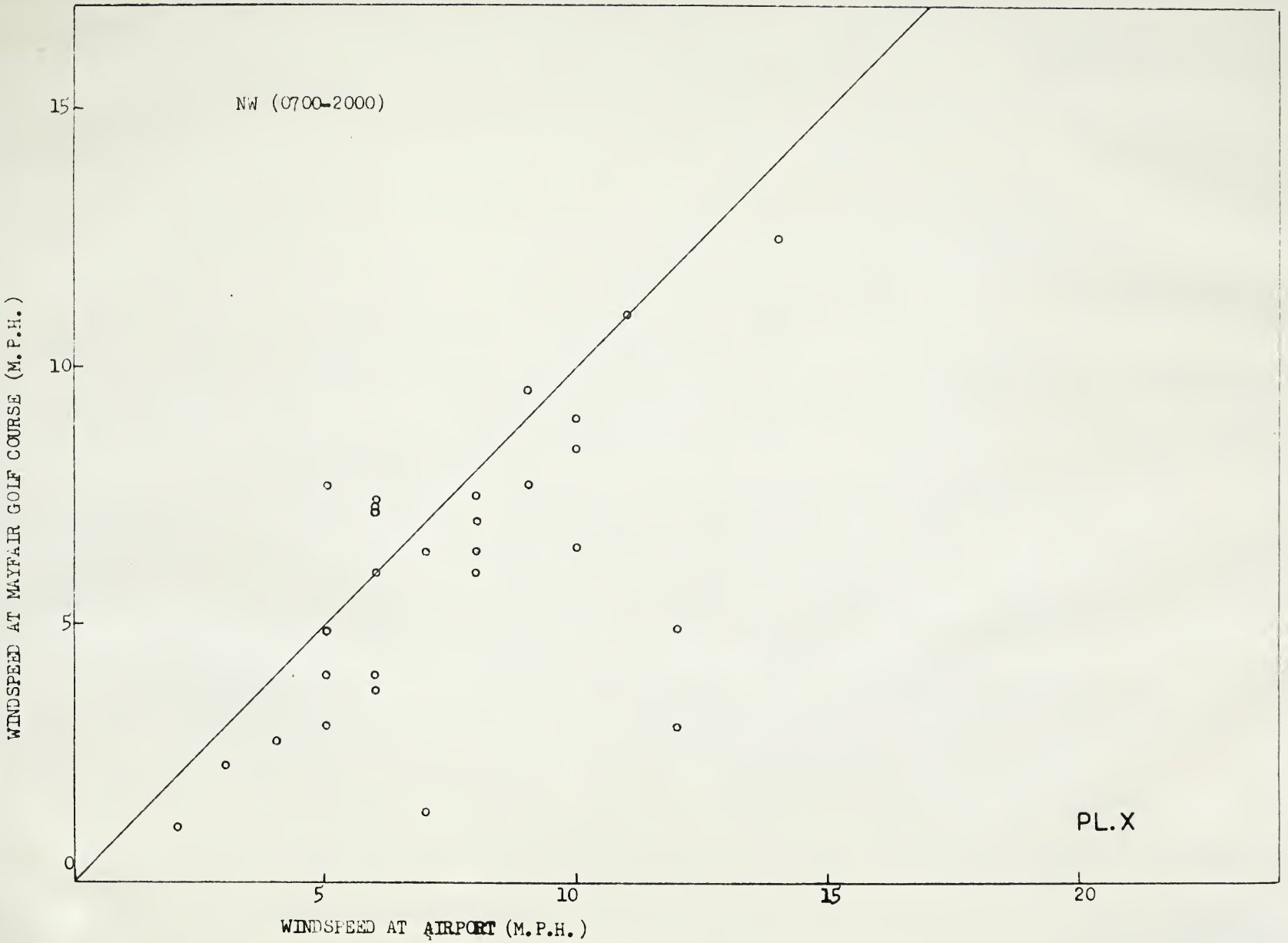
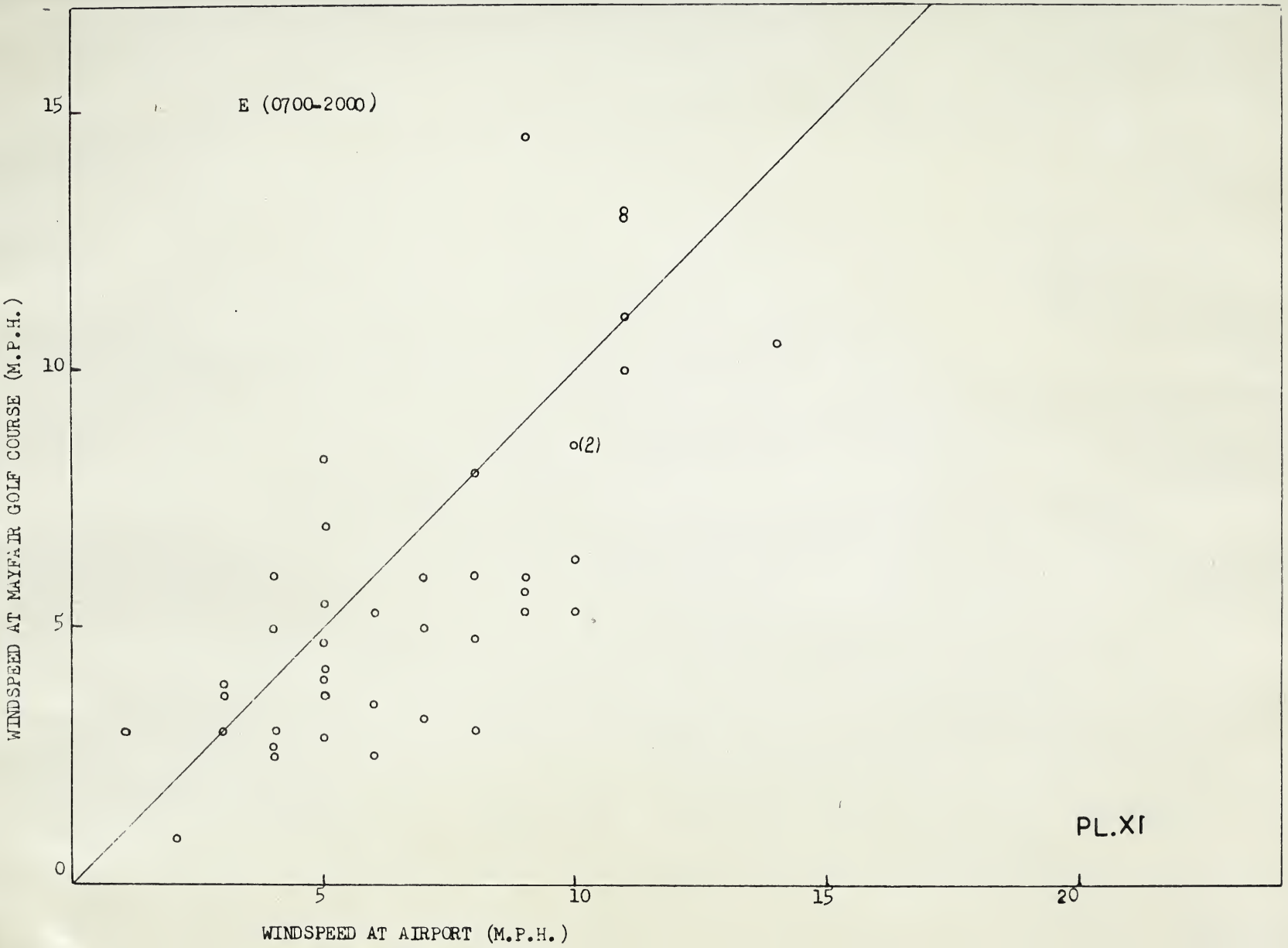
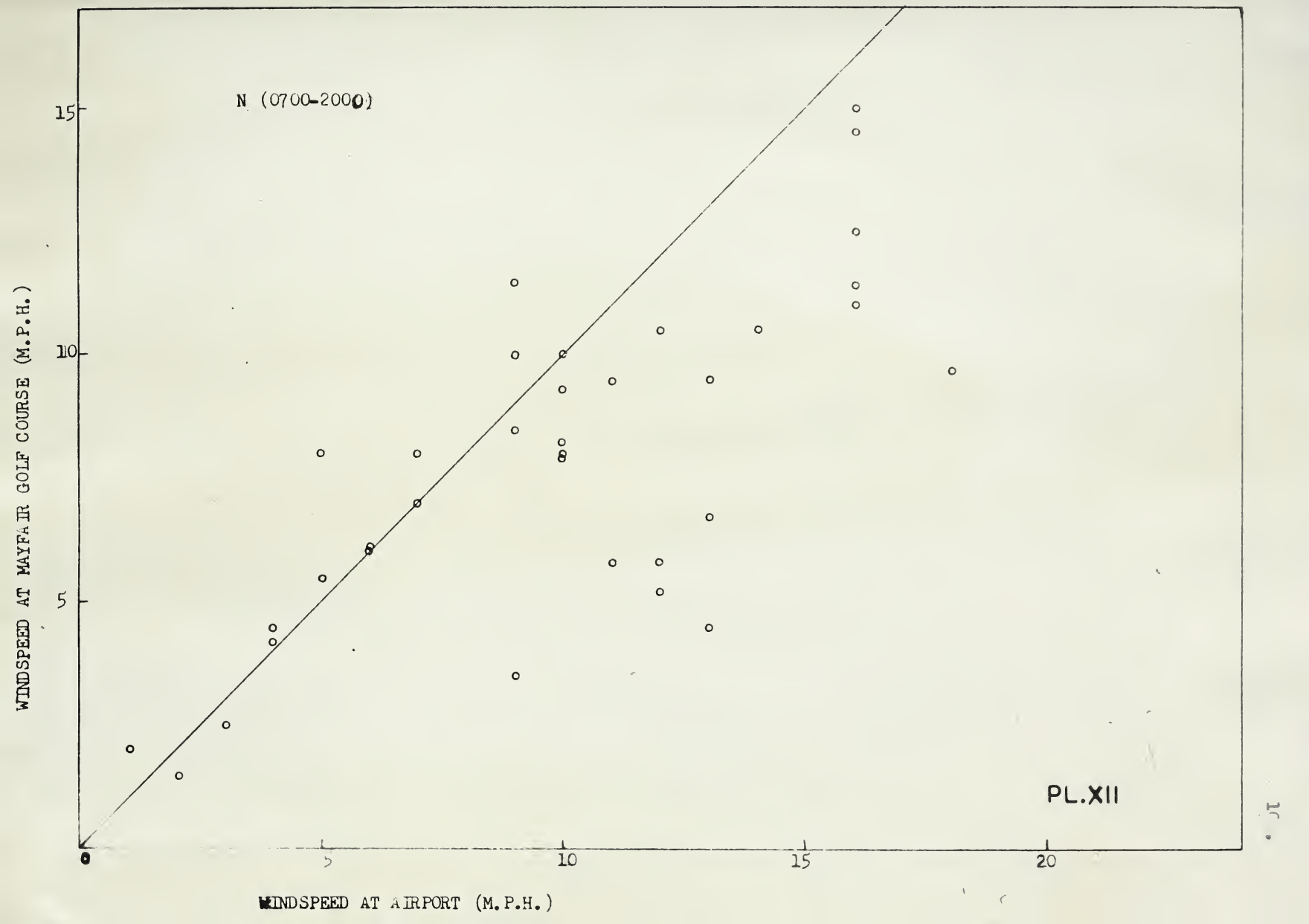
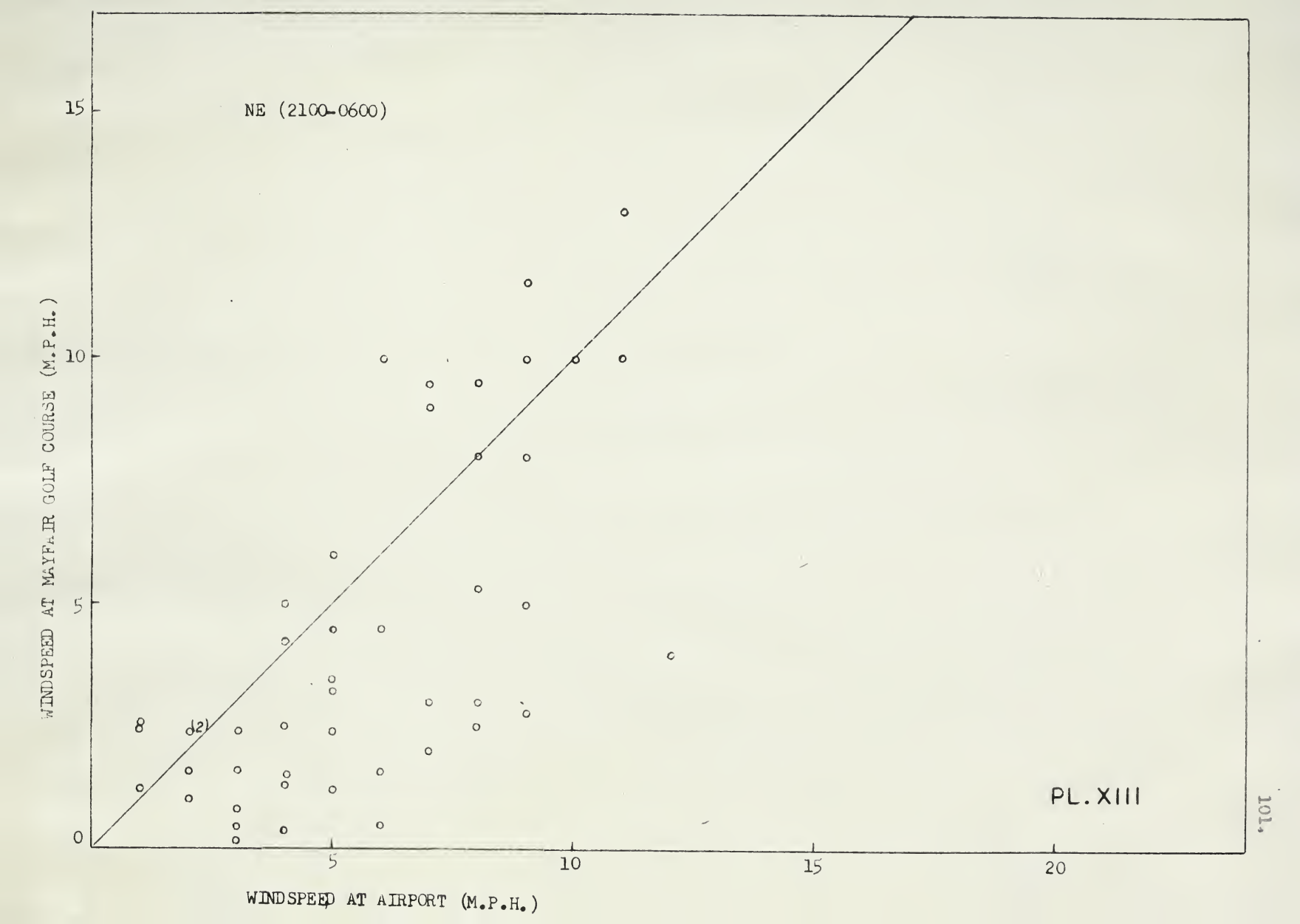
20
PL. VIII


W (0700-2000)
WINDSPEED AT MAYFAIR GOLF COURSE (M.P.H.)
WINDSPEED AT AIRPORT (M.P.H.)
0
5
10
15
20
PL. IX

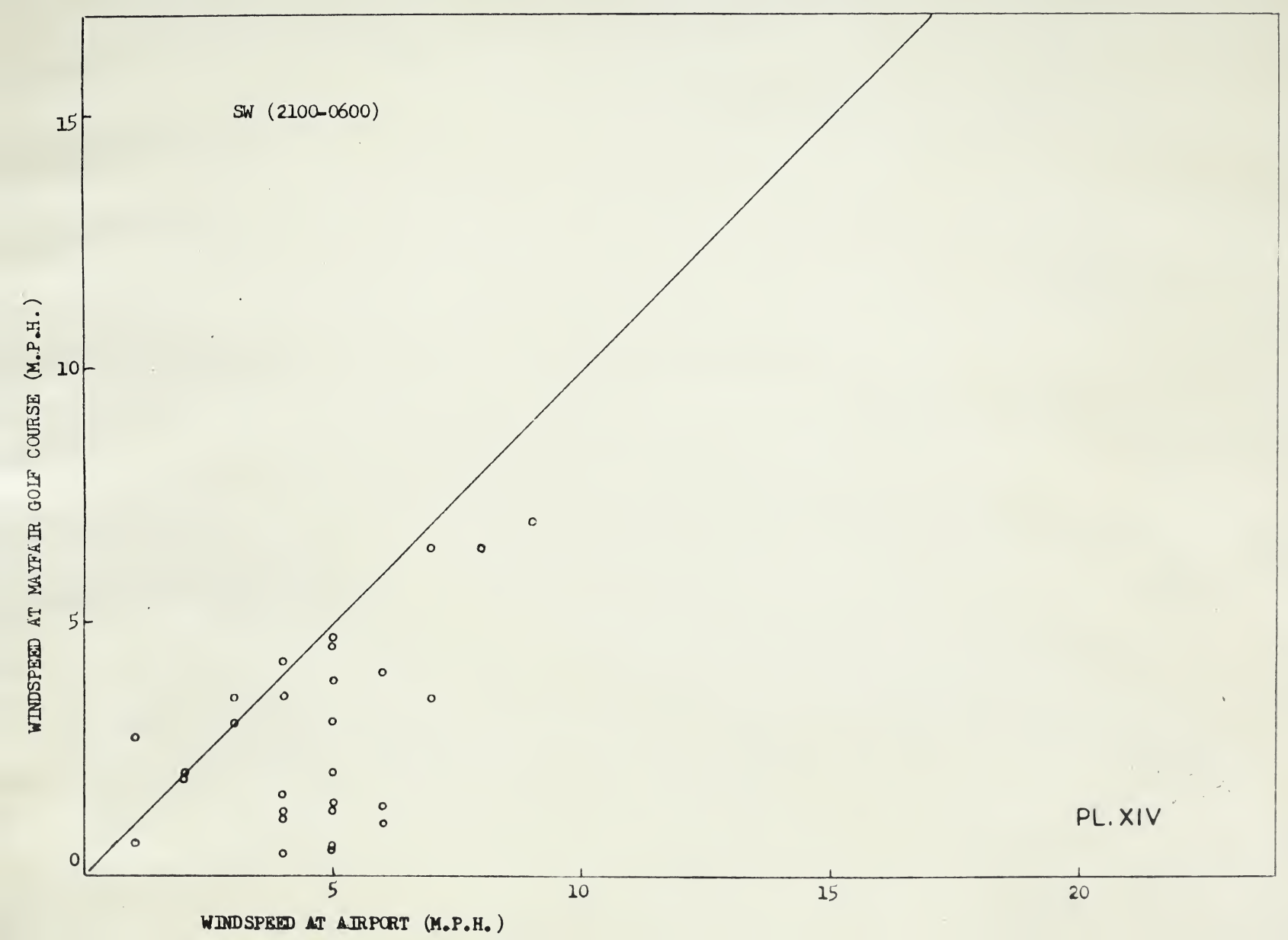

NW (0700-2000)
WINDSPEED AT MAYFAIR GOLF COURSE (M.P.H.)
WINDSPEED AT AIRPORT (M.P.H.)
0
5
10
15
20
PL.X

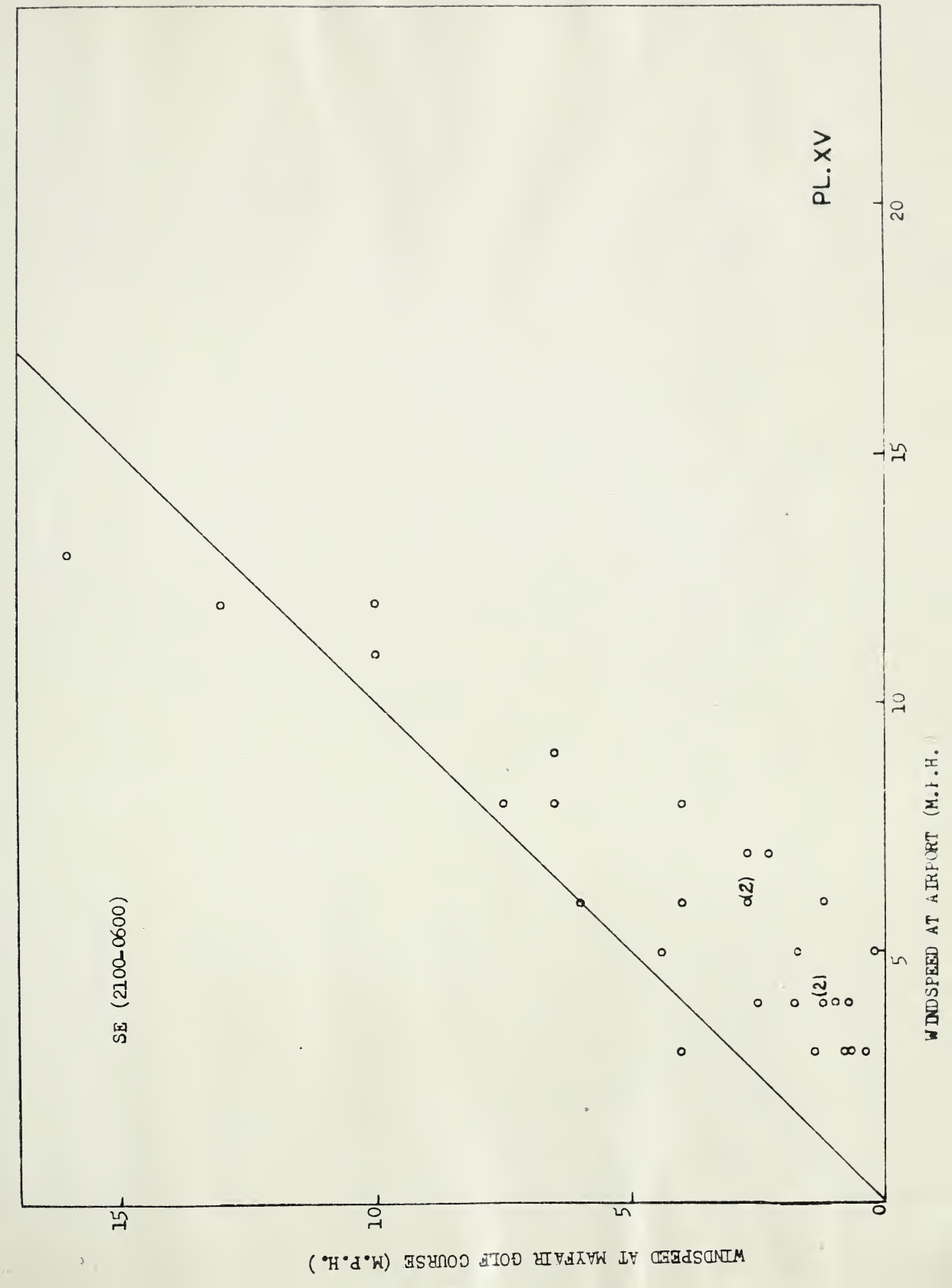

E (0700-2000)
8
(2)
PL.XI
WINDSPEED AT MAYFAIR GOLF COURSE (M.P.H.)
WINDSPEED AT AIRPORT (M.P.H.)
0
5
10
15
20

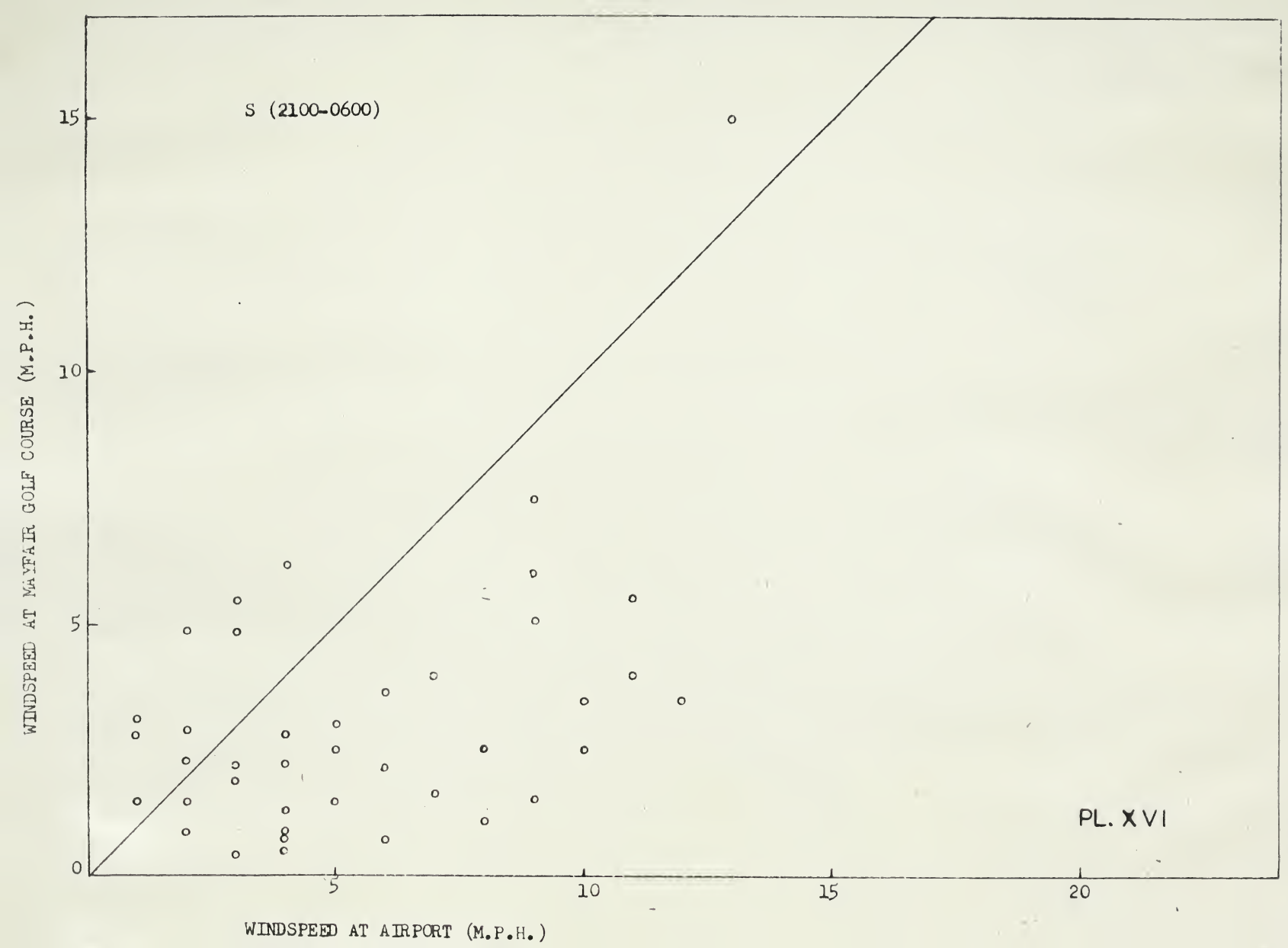

N (0700-2000)
WINDSPEED AT MAYFAIR GOLF COURSE (M.P.H.)
WINDSPEED AT AIRPORT (M.P.H.)
0
5
10
15
20
PL.XII

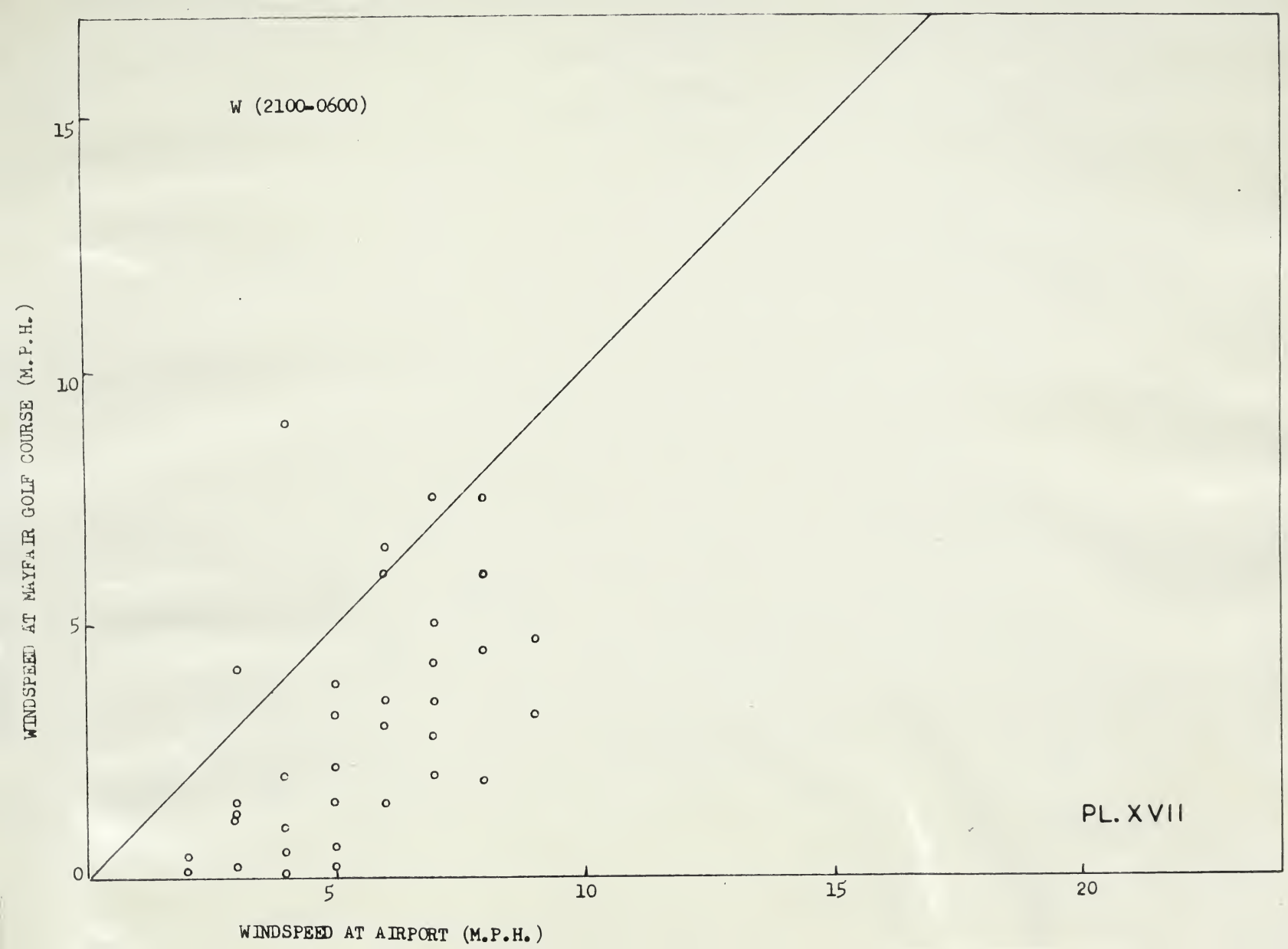

NE (2100-0600)
WINDSPEED AT MAYFAIR GOLF COURSE (M.P.H.)
WINDSPEED AT AIRPORT (M.P.H.)
0
5
10
15
20
8
(2)

PL. XIII

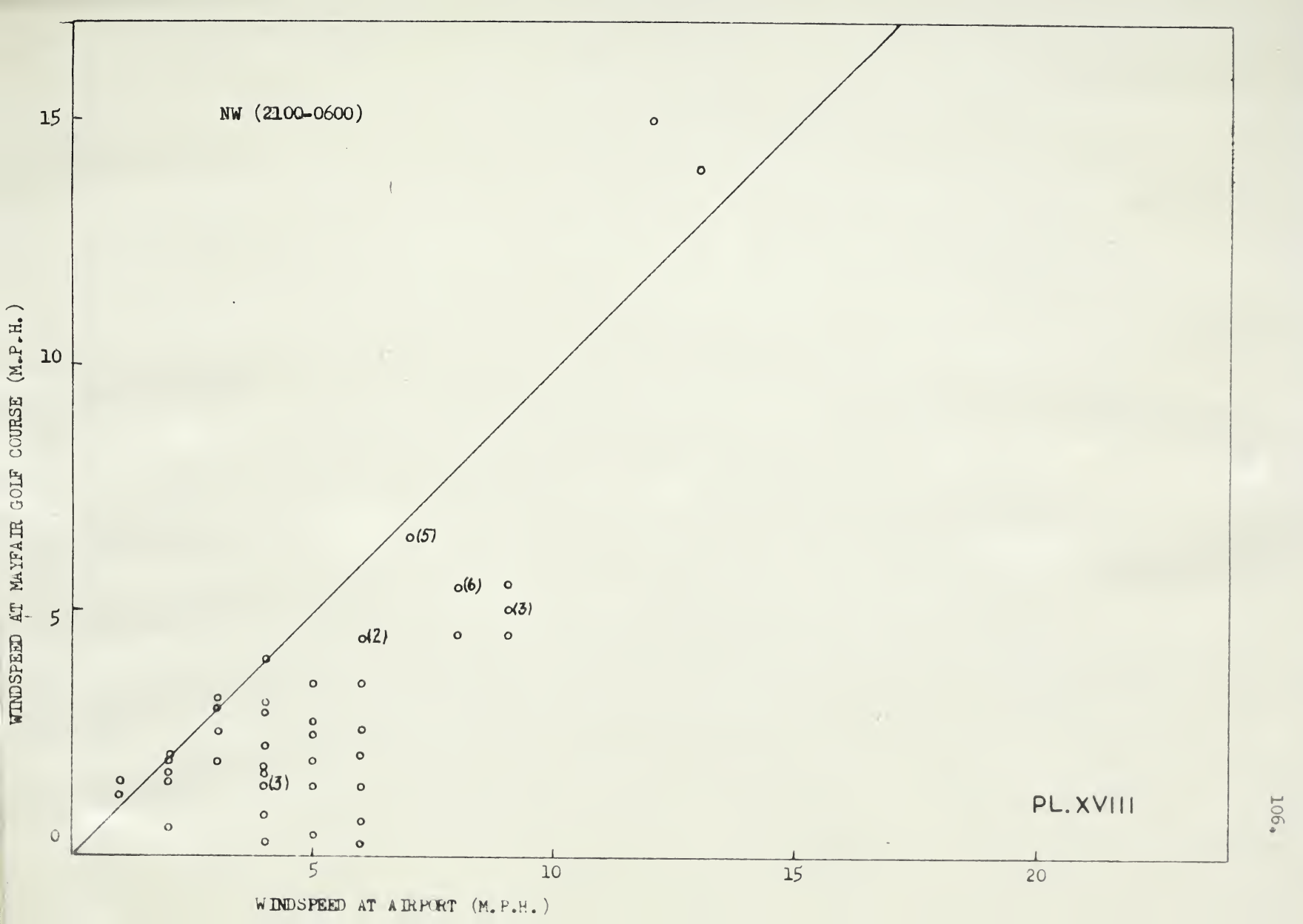

SW (2100-0600)
15
10
5
0
5
10
15
20
WINDSPEED AT MAYFAIR GOLF COURSE (M.P.H.)
WINDSPEED AT AIRPORT (M.P.H.)
PL. XIV

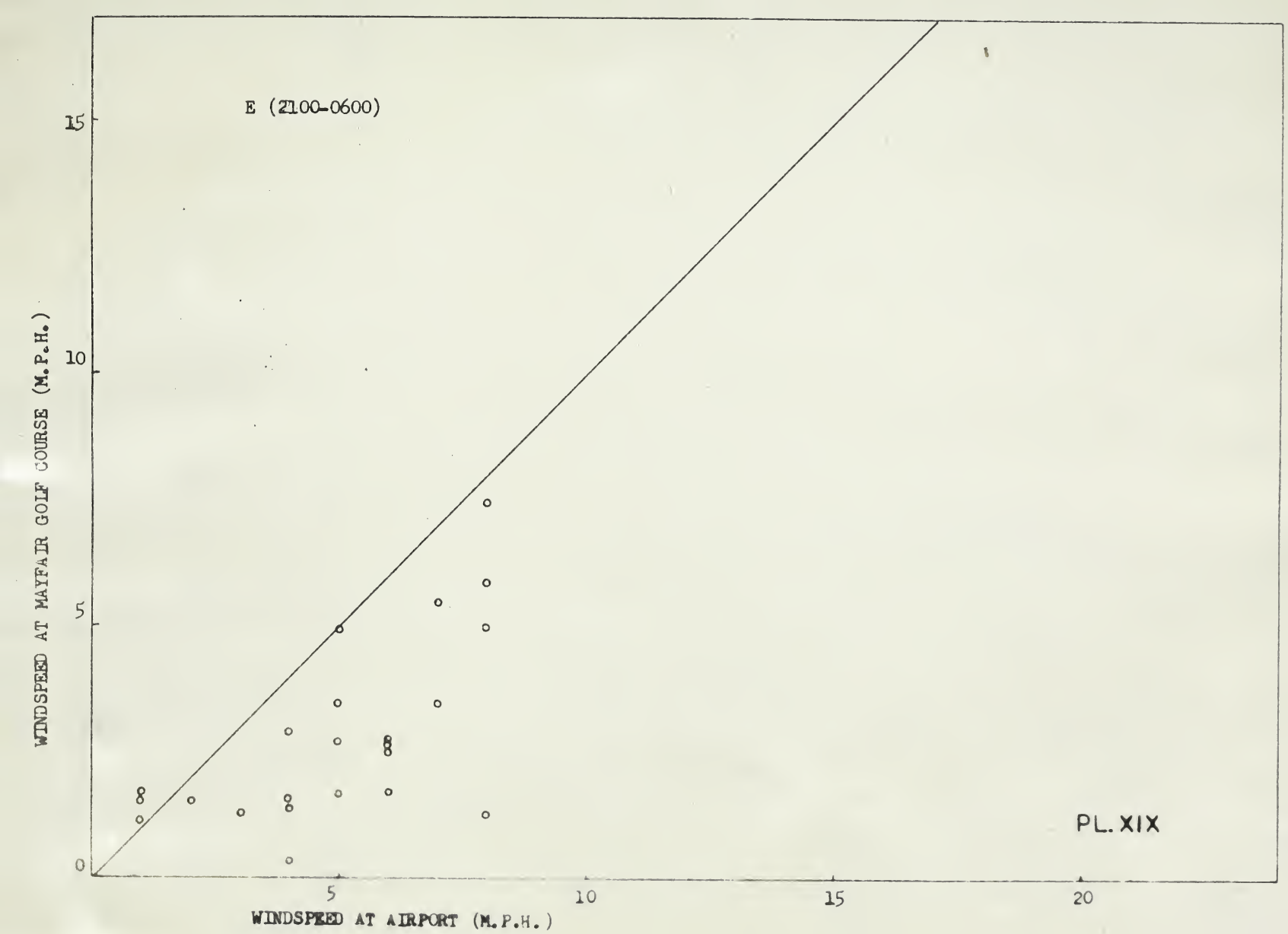

PL.XV
SE (2100-0600)
WINDSPEED AT MAYFAIR GOLF COURSE (M.P.H.)
WINDSPEED AT AIRPORT (M.P.H.)
0
5
10
15
20
(2)
(2)

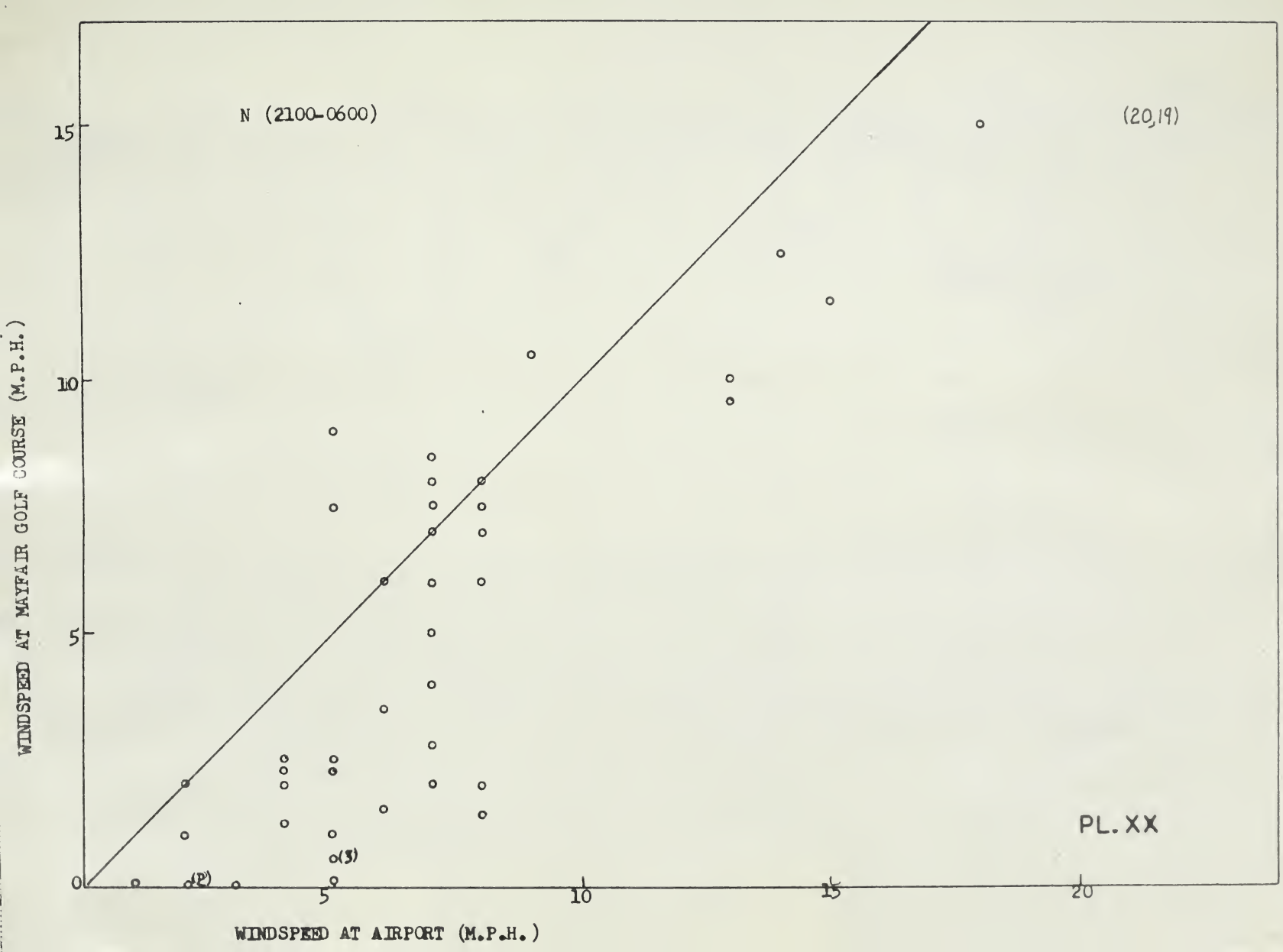

S (2100-0600)
15
10
5
0
5
10
15
20
WINDSPEED AT MAYFAIR GOLF COURSE (M.P.H.)
WINDSPEED AT AIRPORT (M.P.H.)
PL. XVI

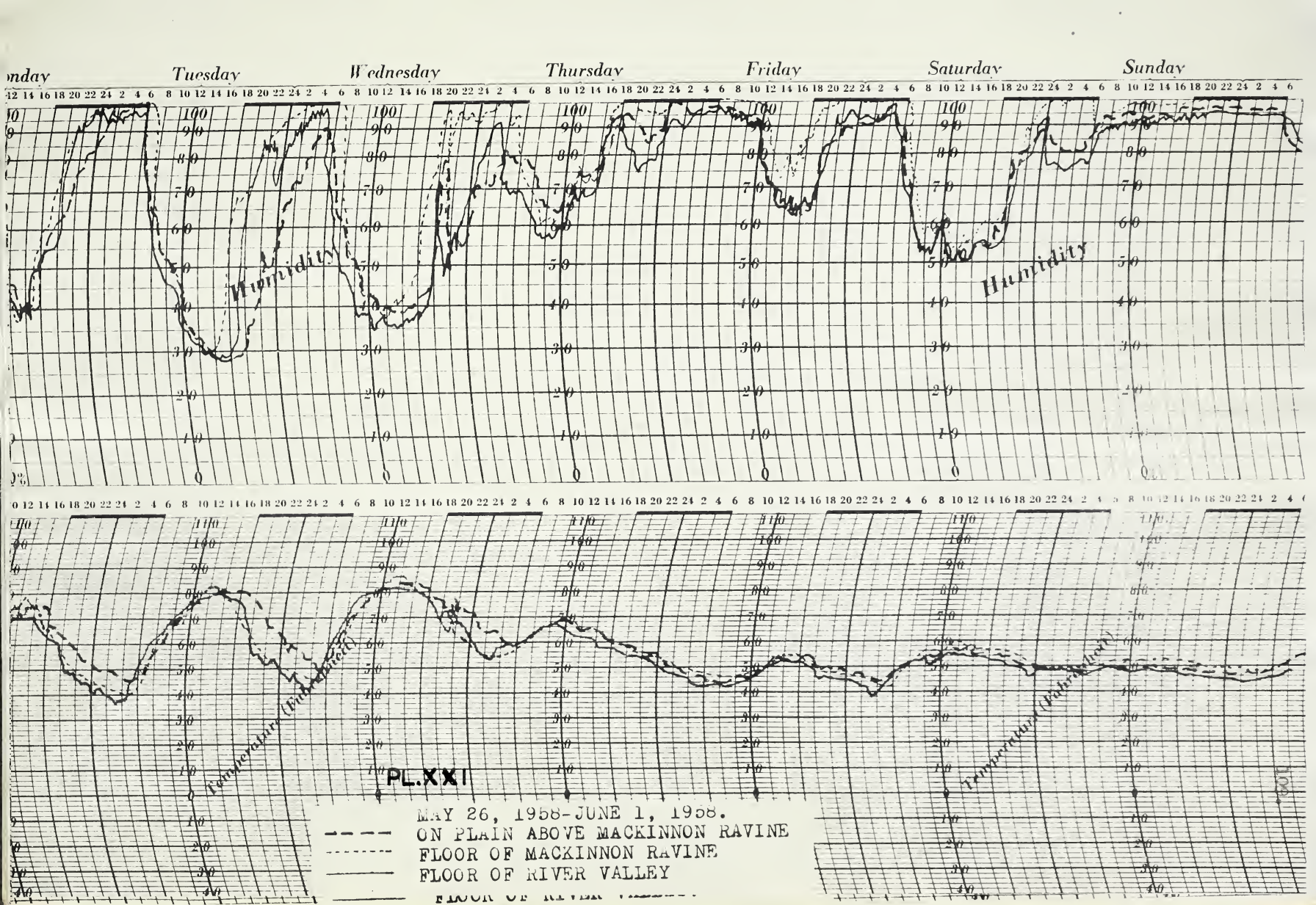

W (2100-0600)
WINDSPEED AT MAYFAIR GOLF COURSE (M.P.H.)
WINDSPEED AT AIRPORT (M.P.H.)
0
5
10
15
20

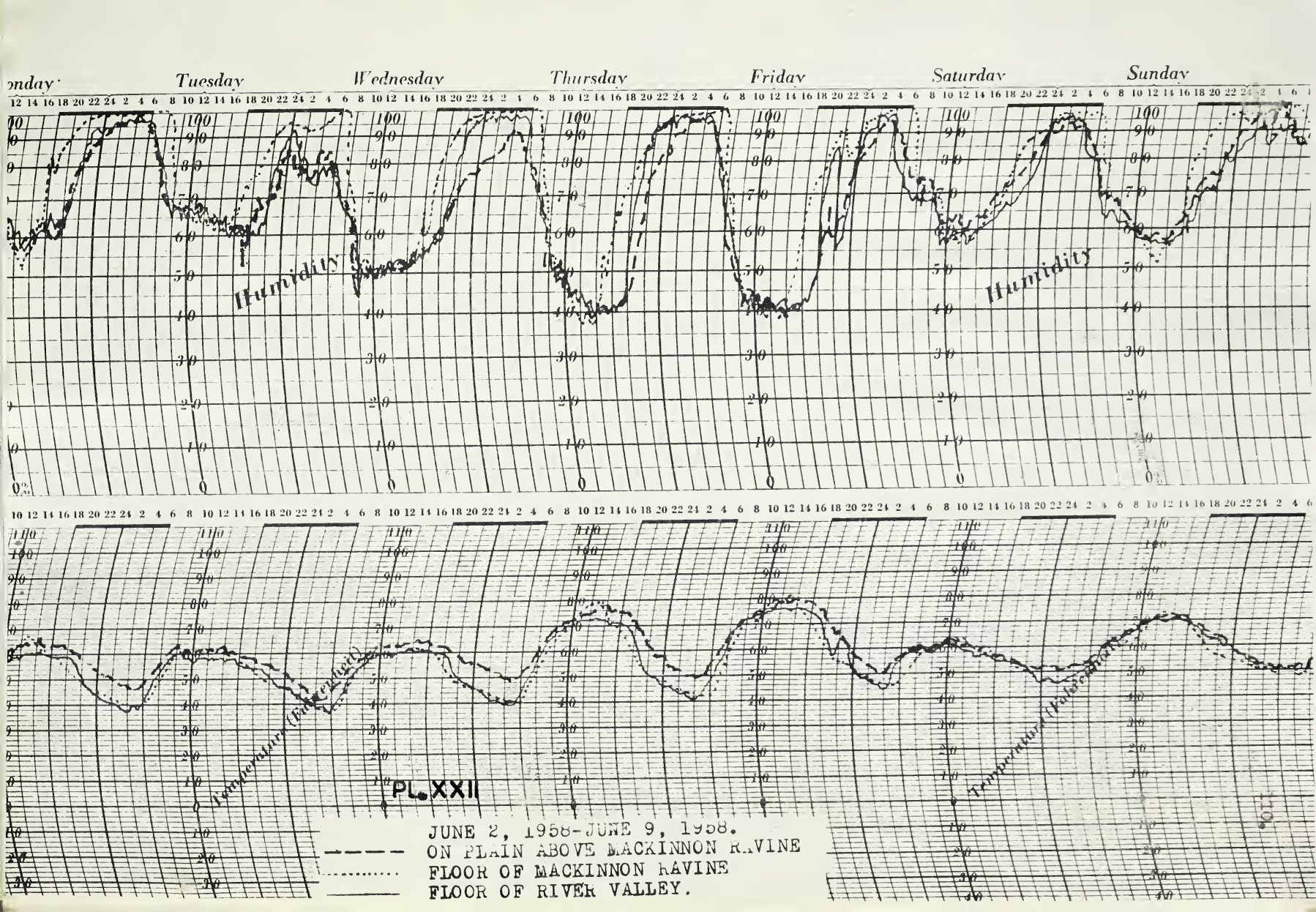
PL. XVII


NW (2100-0600)
WINDSPEED AT MAYFAIR GOLF COURSE (M.P.H.)
WINDSPEED AT AIRPORT (M.P.H.)
0
5
10
15
20
o(5)
o(6)
o(3)
o(2)
o(3)
PL. XVIII


E (2100-0600)
15
10
5
0
5
10
15
20
WINDSPEED AT MAYFAIR GOLF COURSE (M.P.H.)
WINDSPEED AT AIRPORT (M.P.H.)
PL. XIX


N (2100-0600)
(20,19)
15
10
5
0
5
10
15
20
(P)
(S)
WINDSPEED AT MAYFAIR GOLF COURSE (M.P.H.)
WINDSPEED AT AIRPORT (M.P.H.)
PL. XX


nday
Tuesday
Wednesday
Thursday
Friday
Saturday
Sunday
Humidity
Humidity
Humidity
Temperature (Fahrenheit)
Temperature (Fahrenheit)
Temperature (Fahrenheit)
PL.XXI
MAY 26, 1958-JUNE 1, 1958.
ON PLAIN ABOVE MACKINNON RAVINE
FLOOR OF MACKINNON RAVINE
FLOOR OF RIVER VALLEY


Tuesday
Wednesday
Thursday
Friday
Saturday
Sunday
Humidity
Humidity
Temperature (Fahrenheit)
Temperature (Fahrenheit)
PL. XXII
JUNE 2, 1958-JUNE 9, 1958.
ON PLAIN ABOVE MACKINNON RAVINE
FLOOR OF MACKINNON RAVINE
FLOOR OF RIVER VALLEY.

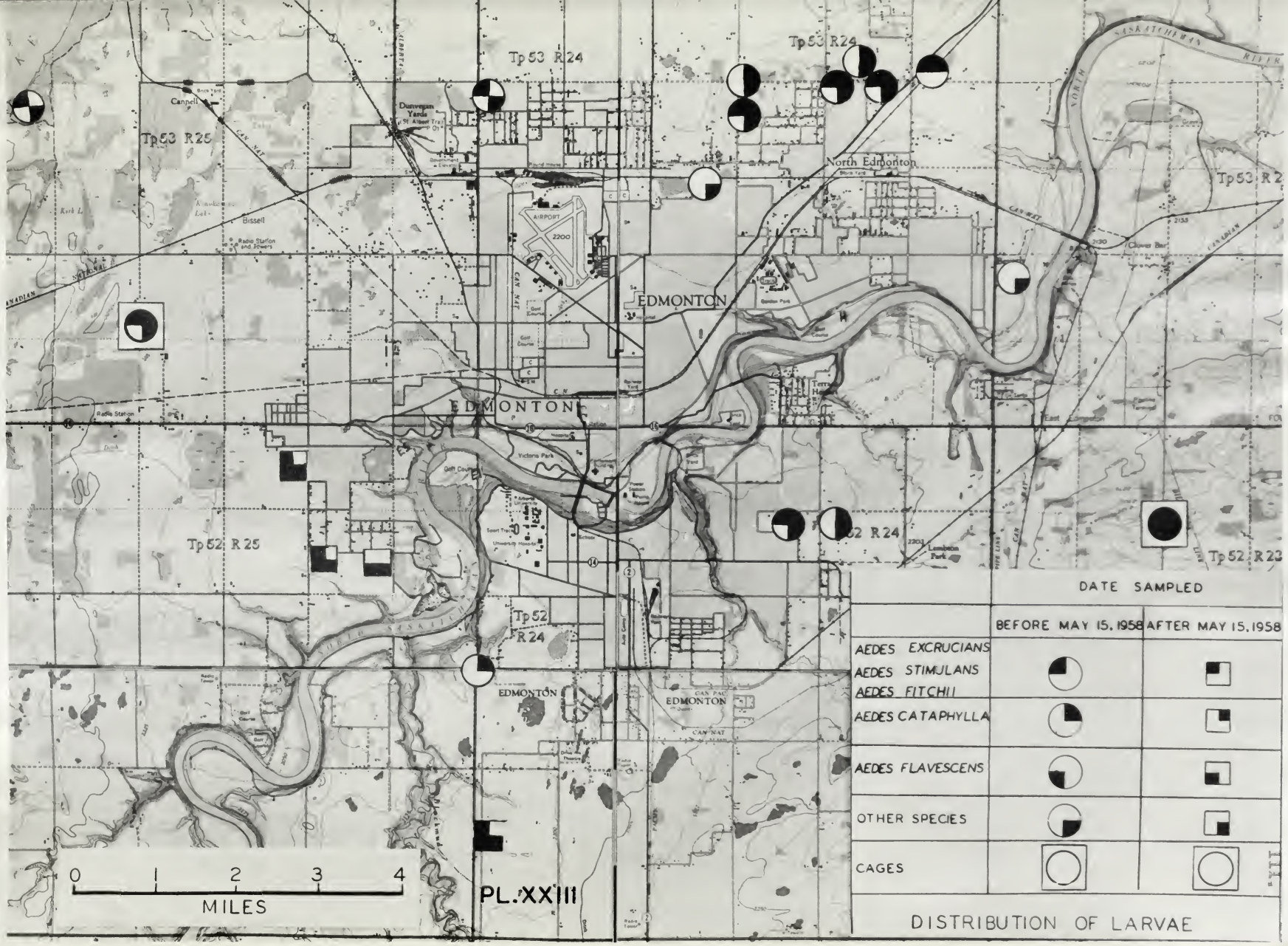

Tp 53 R 24
Tp 53 R 24
Tp 53 R 25
Tp 53 R 2
Tp 52 R 25
Tp 52 R 24
Tp 52 R 23
Tp 52 R 24
Cannell
Dunvegan Yards
Bissell
North Edmonton
EDMONTON
EDMONTON
EDMONTON
EDMONTON
AIRPORT
2200
Victoria Park
Lambton Park
Clover Bar
East Edmonton
CAN NAT
CANADIAN
NORTH SASKATCHEWAN RIVER
0 1 2 3 4
MILES
PL. XXIII
DATE SAMPLED
BEFORE MAY 15, 1958
AFTER MAY 15, 1958
AEDES EXCRUCIANS
AEDES STIMULANS
AEDES FITCHII
AEDES CATAPHYLLA
AEDES FLAVESCENS
OTHER SPECIES
CAGES
DISTRIBUTION OF LARVAE

Table 4. Predicted and observed activity.

	Hour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
May 10	Wind	N	N	N	N	W	SW	W	NW	NW	NW	W	NW	NW	SW	SE	S	NW	E	E	E	E	E	NE	N
		14	11	14	5	5	6	5	8	9	8	8	8	6	17	5	4	2	5	8	9	9	6	6	7
	Temp.	52	52	51	48	46	46	44	47	51	54	55	55	55	59	59	59	59	60	59	59	56	54	54	52
	R. H.	35	35	34	47	58	52	63	53	50	42	38	38	38	33	33	33	33	34	38	38	39	37	53	63
	Cloud.	10	10	9	10	7	7	6	5	7	9	9	9	7	6	7	7	9	6	6	6	10	10	10	10
	Weather	Cldy. lgt. rain late evng. Wnd. fresh Nrly ovrngt. Othwse. lgt. vrbl. 0.02" rain. PLI: 0200 h.-0300 h.																							
	Biology	Buds burst on trees in river valley. One 'blacklegged' mosquito seen.																							
	Activity	L	M	M	L	L	L	L	L	M	M	M	M	M	L	M	M	M	M	M	M	M	M	M	M
May 11	Wind	E	E	NE	E	E	SE	SE	E	E	E	E	SE	SE	E	E	E	E	E	E	NE	E	E	NE	N
		12	12	14	12	8	8	9	9	10	13	16	19	16	14	13	11	11	15	18	13	13	16	13	11
	Temp.	52	51	48	47	46	47	47	46	47	47	49	50	51	55	54	55	57	57	56	54	52	51	48	46
	R. H.	68	73	73	72	72	72	93	86	86	89	59	55	61	51	41	39	36	40	42	49	56	66	60	64
	Cloud.	8	9	10	9	10	10	10	10	8	7	9	9	9	9	9	9	10	10	10	10	10	9	9	9
	Weather	Cldy. to ovc. Lgt. rain ovrngt. and evng. Wind ENE-ESE, fresh midday. Active cold front approaching. 0.1" rain. PLI: 0100 h.-0200 h.																							
	Biology	3 ♀♀: E5(0100h.-2400 h.)																							
	Activity	M	M	L	L	L	L	L	L	L	L	L	L	L	L	L	M	M	L	L	L	L	L	L	L

	Hour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
May 12	Wind	N 7	NW 11	NW 20	NW 16	N 12	NW 14	NW 17	NW 18	NW 21	NW 21	NW 24	N 24	N 24	N 25	N 22	N 20	N 25	N 26	N 24	N 21	N 21	NW 16	NW 13	NW 9
	Temp.	52	51	48	47	46	47	47	46	47	47	49	50	51	55	54	55	57	57	56	54	52	51	48	46
	R. H.	75	75	93	86	93	86	86	86	79	72	61	55	50	38	32	33	31	22	16	17	19	17	23	26
	Cloud.	10	10	8	9	10	9	10	10	9	9	8	8	8	7	9	7	9	9	9	9	9	7	5	3

Weather Cldy. to ovc. Intmt. lgt. rain ovrngt. Fresh NWly winds, gusty midday. Trace of rain. Very active cold front passed at 0400 h. PLI: 0100 h.-0200 h.

Biology 1♀

	Activity	M	M	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L

May 13	Wind	NW 9	NW 13	NW 13	NW 10	W 10	W 8	NW 10	NW 12	NW 14	NW 18	NW 20	NW 19	NW 16	NW 14	NW 13	NW 19	NW 7	NW 6	NW 4	NW 4	NW 2	NW 3	S 2	SW 6
	Temp.	42	41	41	40	38	38	38	42	46	50	53	55	58	60	62	63	63	64	65	64	63	58	56	51
	R. H.	40	39	39	37	50	50	42	40	39	38	31	23	23	26	24	25	29	26	27	26	25	37	34	45
	Cloud.	00	0	2	3	3	2	1	1	1	1	1	1	1	2	2	3	3	3	4	2	2	1	1	1

Weather Few hi. clds. Lgt. to fresh W-NWly winds gusty late A.M.

Biology No mosquitoes encountered in city or country.

	Activity	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	M	M

May 14	Hour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
	Wind	SW 7	SW 6	SW 6	SW 6	SW 8	SW 6	SW 6	S 5	S 7	S 14	S 19	S 16	S 19	S 16	S 17	S 17	S 17	S 16	S 17	S 14	S 12	S 14	S 17	S 16
	Temp.	44	46	45	44	43	42	45	48	53	64	68	70	70	72	74	74	75	73	72	70	67	64	61	60
	R. H.	48	58	57	56	55	62	57	54	52	38	27	25	25	24	26	26	27	29	31	33	33	38	40	48
	Cloud.	1	1	2	3	6	4	4	3	5	9	9	10	10	10	10	8	8	9	9	9	8	5	3	3
	Weather	Vrbl. hi clds. Lgt. S-SSWly winds, fresh aftn. and evng.																							
	Biology																	1♀						1♂	
	Activity	L	L	L	L	L	L	L	L	M	M	L	L	L	L	L	L	L	L	L	L	L	L	L	L

May 15	Wind	S 15	S 15	S 14	S 10	S 8	S 9	SW 6	W 8	W 10	NW 10	NW 9	W 7	W 9	W 8	SW 9	SW 6	SW 10	SS 9	S 10	S 11	S 7	S 8	S 10	S 9
	Temp.	57	56	55	53	48	47	47	52	62	66	69	70	73	75	76	76	76	77	76	76	73	70	66	62
	R. H.	50	50	54	52	66	66	72	69	41	29	24	29	25	24	24	25	18	18	21	20	22	32	35	33
	Cloud.	3	3	3	4	5	6	6	8	10	10	10	10	9	9	9	7	7	6	6	6	7	7	7	7
	Weather	Vrbl. thin hi. clds. Wind vrbl. S-WNW, lgt. ocnly. fresh.																							
	Biology	2100 h.:biting at E5.														1♀				2♀♀		3 ♀♀	1♂,1♀	2♀♀	
	Activity	L	L	L	M	L	L	L	M	M	L	L	L	L	L	L	L	L	L	L	L	L	L	M	M

	Hour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
May 16	Wind	W 7	NW 14	N 21	N 30	N 25	NW 14	NW 21	NW 28	NW 29	NW 25	NW 25	NW 25	NW 28	NW 25	NW 25	NW 27	N 26	N 25	N 25	N 22	N 16	NW 14	NW 9	NW 10
	Temp.	62	60	59	58	55	51	51	53	52	54	56	57	59	59	61	61	60	60	60	58	56	53	52	50
	R. H.	32	34	38	41	43	45	45	36	40	32	30	26	24	24	22	22	21	26	26	23	30	36	35	43
	Cloud.	7	6	7	9	9	7	7	5	2	2	2	2	3	5	5	5	5	5	5	4	6	6	7	8
	Weather	Vrbl. cldns. Lgt. shwr erly A.M. Fresh gusty NNWly winds. Trace of rain.																							
	Biology	2♀♀							1♀															1♀	
	Activity	M	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	M	M
May 17	Wind	NW 14	NW 14	NW 17	NW 17	NW 16	NW 17	NW 16	NW 18	NW 20	NW 23	NW 23	NW 20	NW 20	NW 20	NW 20	NW 20	NW 20	N 16	N 17	N 15	N 9	N 6	N 7	NW 5
	Temp.	50	48	47	46	45	44	45	47	51	54	55	58	58	59	60	62	61	61	61	59	57	53	50	48
	R. H.	38	41	40	45	51	49	51	46	39	42	33	27	27	29	30	24	27	18	22	29	31	36	38	41
	Cloud.	4	0	0	1	1	1	1	0	1	3	4	6	6	6	6	6	6	6	2	1	1	1	1	0
	Weather	Cldy. aftn. Fresh gusty NNWly winds.																							
	Biology	1♀ 2♀♀ 10♀♀ 1♀ 17♀♀ and 3 ♂♂: E5 (0800 h.-1900 h.) 6 ♀♀ and 1 ♂: E5 (1900 h.-2400 h.) Five ♀♀: E1 (0100 h.-2100 h.) Huge swarms at E5 and E1.																							
	Activity	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	M	M	L

	Hour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
May 25	Wind	S	SW	SW	NW	NW	N	N	N	NW	NW	NW	NW	NW	NW	NW	NW	N	N	N	N	N	N	N	N
		9	10	8	11	16	20	18	23	21	23	26	26	29	27	29	30	28	27	28	19	13	10	8	10
	Temp.	63	59	57	56	60	60	56	57	58	61	63	64	67	67	66	65	65	67	66	63	61	59	56	53
	R. H.	60	67	71	71	48	48	60	50	46	31	29	30	26	26	32	32	32	26	32	32	43	47	47	52
	Cloud.	0	0	1	3	5	4	3	2	1	0	0	1	7	7	7	5	6	5	4	4	4	5	5	2
	Weather	Ocnly. cldy. aftn. Fresh gusty WNWly winds. Very peppy cold front passed at 0353 h. PLI: 2200 h.-2400 h.																							
	Biology	6♀♀, 6 ♂♂: E5 (1900 h.-2100 h.) Late P.M.: many A. cataphylla swarms along ravines.																							
	Activity	M	M	M	M	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	M	M	M
May 26	Wind	N	NE	W	W	W	W	SW	SW	W	W	NW	NW	N	N	N	N	N	E	NE	E	E	E	SW	W
		9	3	5	6	6	2	1	3	2	3	7	7	13	18	15	13	20	18	22	10	5	2	3	4
	Temp.	51	51	49	48	48	47	48	51	56	59	62	64	64	68	68	69	70	72	65	63	60	58	55	54
	R. H.	62	62	67	66	73	72	79	68	60	52	41	38	31	31	28	29	24	39	42	48	48	51	59	64
	Cloud.	7	8	9	9	8	8	7	7	7	5	5	7	9	9	5	3	4	6	6	9	8	7	7	7
	Weather	Sctd. cu. hier sctd. to brkn. hi cld. Lgt. R shwr. A.M. Lgt. vrbl. winds.																							
	Biology																			1♀			1♀		
	Activity	M	M	L	L	L	L	L	M	M	M	M	M	L	L	L	L	L	L	L	M	M	M	M	M

	Hour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
May 27	Wind	W 1	W 3	SW 4	SW 5	SW 3	SW 3	SW 2	S 2	SW 4	S 4	S 4	SW 5	SW 6	SW 6	SW 6	SW 5	SW 7	SW 7	S 6	S 5	S 6	SW 9	SW 8	SW 11
	Temp.	51	50	49	47	45	45	50	55	58	62	65	69	72	74	77	78	80	80	79	79	77	73	67	65
	R. H.	68	67	73	79	78	86	74	65	56	50	44	39	31	26	<20	<20	<20	<20	<20	<20	26	46	59	64
	Cloud.	4	5	5	4	4	3	2	2	2	9	9	6	8	8	8	6	6	6	6	6	6	6	6	4
	Weather	Vrbl. hi. clds. Lgt. vrbl. winds. PLI: 2200 h.-2400 h.																							
	Biology	2♀♀: E5 (2400 h.-1200 h.) Many swarms of A. cataphylla mosquitoes along White Mud Creek.																			1♀	2♀♀	4♀♀		
	Activity	M	M	L	L	L	L	M	M	M	M	M	M	M	L	L	L	L	L	L	L	L	M	M	M
May 28	Wind	W 6	W 3	SW 5	W 4	SW 3	N 7	SW 2	E 4	E 7	E 6	E 10	SE 11	SE 9	SE 9	E 11	E 10	E 13	E 13	E 12	E 11	SE 8	SE 12	SW 4	SE 4
	Temp.	63	61	58	54	52	52	55	61	65	69	73	78	79	79	82	82	83	83	82	80	78	75	74	74
	R. H.	42	49	56	64	69	69	65	54	44	28	39	27	27	28	<20	<25	<20	<20	<20	32	33	44	43	36
	Cloud.	3	3	3	3	4	3	5	7	9	10	10	4	8	8	10	10	10	10	10	10	10	10	10	10
	Weather	Increasing hi. clds. Incrsg. CB evng. Tstm. evng. Wind gnrly. lgt. and vrbl.																							
	Biology	1♂: E1(2400 h.-1000 h.) Swarms on Riverside G. C. at 2000 h., A. cataphylla and A. fitchii.																							
	Activity	M	M	M	M	M	M	M	M	M	M	M	L	L	M	L	L	L	L	L	L	M	L	M	M

	Hour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
May 29	Wind	E	SE	S	NE	NE	E	E	E	E	E	E	E	NE	E	E	E	SE	SE	N	NE	NE	NE	NE	NE
		5	4	5	4	9	14	15	17	18	19	18	18	17	13	10	10	6	3	5	11	10	9	11	14
	Temp.	70	64	65	66	62	57	58	60	62	64	67	67	67	65	65	65	63	63	61	60	57	56	55	55
	R. H.	44	56	52	48	59	66	66	63	50	47	41	41	49	52	52	52	55	55	63	72	82	76	70	70
	Cloud.	10	9	8	9	9	9	8	9	9	9	10	10	10	10	10	10	10	10	10	10	10	9	10	10

Weather Cldy. to ovc. Shwrs. aftn. Lgt. rain evng. Wind lgt. vrbl. xcpt. fresh and vrbl. ENE-ESE during day. Cold front passed at 1200 h.; 48 hrs. prior many thunderstorms.

Biology 1♀: E5 (2100 h.-2200 h.)

	Activity	M	M	M	M	M	L	L	L	L	L	L	L	L	M	M	M	M	M	M	M	M	H	H	L

May 30	Wind	NE	NE	NE	NE	NE	NE	NE	NE	NE	NE	NE	NE	NE	NE	E	NE	E	NE	N	N	N	N	N	N
		10	16	18	17	18	20	24	20	20	15	14	14	18	17	11	7	5	6	6	6	6	5	7	4
	Temp.	54	52	49	48	47	46	45	44	43	43	44	45	45	46	48	51	51	53	54	54	53	51	49	49
	R.H.	76	81	86	86	86	93	93	93	100	100	93	86	93	86	66	68	68	58	48	53	63	62	80	80
	Cloud.	10	10	10	10	10	10	10	10	10	10	10	10	10	9	9	8	6	6	4	6	7	8	8	8

Weather Ovc. with lgt. rain ending at noon. Cldy. aftn. Fresh ocnly. gusty NEly winds lgt. evng.

Biology 1♀: E1 (0700 h.-1200 h.) 1♀
Much emergence in rearing cages.

	Activity	M	L	L	L	L	L	L	L	L	L	L	L	L	L	L	M	M	M	M	M	M	M	L	L

Table 4. Predicted and observed activity.

	Hour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
May 31	Wind	SE 3	SW 6	SW 6	SW 5	SW 4	SW 4	S 5	S 8	S 10	S 14	S 15	S 15	S 15	S 15	SE 13	S 14	S 14	S 15	SE 13	SE 11	SE 9	S 10	S 8	S 6
	Temp.	49	47	46	45	44	44	46	48	50	51	53	54	53	54	56	57	57	55	55	55	55	54	52	52
	R. H..	73	86	93	93	93	93	86	79	67	62	47	48	52	53	44	40	40	43	49	43	43	53	69	69
	Cloud.	9	8	6	9	9	9	9	9	9	10	8	9	9	8	8	7	8	9	9	9	9	9	9	8
	Weather	Cldy. lgt. SWly to fresh SEly winds. Rain late evng. PLI: 2000 h.-2400 h.																							
	Biology																			1 ♀				1 ♀	
	Activity	L	L	L	L	L	L	L	L	M	L	L	L	L	L	L	L	L	L	L	M	M	M	M	M
June 1	Wind	S 6	S 8	S 7	SE 7	SE 5	E 5	SE 6	S 6	SE 5	E 5	NE 9	E 9	E 9	E 10	E 10	E 11	NE 11	NE 11	NE 11	NE 6	NE 4	N 4	N 5	N 5
	Temp.	51	50	51	51	50	50	49	49	49	48	49	49	50	50	50	50	50	50	49	49	49	48	48	48
	R. H.	75	74	68	68	74	80	80	80	80	86	86	86	87	87	87	87	87	87	87	87	86	86	93	93
	Cloud.	8	9	9	9	9	9	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	99	9	10
	Weather	Ovc. with lgt. rain begn. 0623. Lgt. ocnly. fresh SE-NEly. winds. 0.58" rain.																							
	Biology		1 ♀	1 ♀							1 ♀ : El (0900 h.-2100 h.)														
	Activity	M	M	M	M	M	M	L	L	L	L	L	L	M	M	M	M	M	M	L	L	L	L	L	L

June 2	Hour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
	Wind	N 4	N 5	N 2	N 2	N 1	N 2	N 2	N 1	E 2	S 2	SE 3	E 3	NE 4	E 5	E 5	E 5	W 5	NW 6	NW 2	W 5	SW 5	SW 6	S 7	W 5
	Temp.	48	47	47	46	47	47	47	48	49	51	52	55	58	58	60	61	61	61	60	61	60	58	55	53
	R.H.	86	93	93	100	86	93	93	86	86	81	75	76	66	66	51	48	54	49	58	54	58	66	75	81
	Cloud.	10	10	9	9	9	10	9	9	8	9	8	9	8	7	7	7	7	7	6	2	1	1	1	1
	Weather	Ovc. lgt. rain endd. 0515 h., then cldy. clrg. evng. Lgt. vrbl. winds. Trace of rain. PLI: 2100 h.-2400 h.																							
	Biology			5 ♀♀		5 ♂♂ (2400 h.-0900 h.)								1 ♀								1♀, 2♂♂			
		A. M. Many biting mosquitoes in MacKinnon Ravine. Late P.M. Few mosquitoes at White Mud Creek.																							
	Activity	L	L	L	L	L	L	L	L	L	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
June 3	Wind	W 5	W 5	W 2	W 4	W 3	NW 4	NE 2	NW 5	N 10	N 16	NE 14	NE 17	NE 16	NE 17	NE 16	NE 15	NE 15	NE 15	NE 11	NE 7	NE 4	NE 3	NE 3	N 5
	Temp.	50	49	48	47	45	44	46	51	54	58	56	57	58	56	58	58	57	58	56	56	56	54	53	51
	R.H.	87	86	93	93	93	100	93	75	76	66	65	61	61	65	61	56	55	55	55	55	55	63	64	68
	Cloud.	1	1	1	3	2	3	2	5	2	9	9	6	9	9	8	9	9	9	9	8	7	8	8	8
	Weather	Cldy. aftn. and eveng. Lgt. Wly to fresh NNEly, A.M., bcng. lgt. evng.																							
	Biology					1 ♀: E1 (0900 h.-2300 h.)														*		8♂♂, 1♀ 1♂ 2♂♂			
	Activity	M	L	L	L	L	L	L	M	M	L	L	L	L	L	L	L	L	L	M	M	M	M	M	M

Symbols and Abbreviations.

* E5 not operating; 1500 h.-2000 h. inclusive
PLI Possible lunar influence
R.H. Relative humidity
Cloud. Cloudiness in tenths
Temp. Temperature in degrees F.
Activity. Predicted Activity.
In the row designated Biology, ♂ and ♀ refer to Aedes mosquitoes taken in the traps E1 and E5.
Weather data from airport.

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